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SYSTEMATICS OF THE CRAWFISHES OF THE HAGENIANUS GROUP OF THE GENUS *PROCAMBARUS*, SUBGENUS *GIRARDIELLA* (DECAPODA, CAMBARIDAE)

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ABSTRACT

The Hagenianus Group of the crawfish genus *Procambarus* represents those members of the subgenus *Girardiella* which occur east of the Mississippi River and south of the Ohio River. Standard taxonomic procedures and morphometric analyses revealed that there are five distinct species, four of which are new [named *P. (G.) barbiger, P. (G.) cometes, P. (G.) connos,* and *P. (G.) pogum*], and that *P. hagenianus* exists as two subspecies, one previously undescribed and herein named *vesticeps.* The most conspicuous feature of the undescribed taxa is a beard of setae along the mesial margin of the palm, especially in Form I males. Significant morphological distinctions exist in the first pleopods of males, in the annuli ventrales of females, in the chelipeds and in the antennal scales. The group is nearly unique in possessing stout spines which extend beyond the distal margin of the mesial ramus of the uropods; it is unique in the subgenus in that all members lack a cephalic process on the first pleopod. Data suggest close relationships with *P. (G.) tulanei* Penn and a single invasion of their present habitats from the north via the upper coastal plain. There is no evidence of clinal variation, and the species are neither more nor less variable, inter- or intraspecifically, than other crawfishes similarly studied.

The first record of the existence of the crawfishes currently assigned to the subgenus *Girardiella* was the publication of a figure and a description of a single specimen of a Form I male from "Charleston, South Carolina [U.S.A.]" mistakenly identified as *Cambarus carolinus* of Erichson (1846) in Hagen's monograph (1870). The next extensive treatment of the North American crawfishes was by Faxon (1884); it noted the misidentification of the specimen and asserted that it represented an undescribed species. Faxon proposed the name *Cambarus hagenianus* for the species (p. 141), and the single Form I male became the type by monotypy. Following receipt of additional specimens from State College (Oktibbeha Co.) and Muldon (Monroe Co.), Mississippi, and Farmdale (prob. Faunsdale, Marengo Co.), Alabama, he published additional descriptive information, observations on variation and color illustrations of Muldon specimens (Faxon, 1914:366-367, Pl. 1). Among the morphological variations mentioned, the most prominent feature, perhaps, was the bearding of the hand seen in Muldon males. No further taxonomic data on the Hagenianus Group were published until Lyle (1938) presented an abstract of the dissertation he submitted to Iowa State University. In the abstract he alluded to the existence of four distinct breeding populations by the publication of subspecific *nomina nuda;* at the same time he proposed the subgenus *Girardiella* to receive these and the nominate subspecies of *C. hagenianus* Faxon. The species was assigned without comment to the genus *Procambarus* by Hobbs (1942a) when he elevated most of Ortmann's (1905a, 1905b, 1906) subgenera of *Cambarus* to generic rank. Later, in a revision of the genus

Procambarus, he accepted *Girardiella,* refined its definition and assigned additional taxa to the subgenus (Hobbs, 1972a). Nomenclatorial and taxonomic data on the described taxa were amply presented in the paper. Fitzpatrick (1968) gave a preliminary report of the status of the several taxa mentioned by Lyle *(op. cit.),* and in a later paper he summarized the results here presented in proper taxonomic detail, along with observations on the general biology and economic impact of the several taxa (1975). In the same paper he proposed that the subgenus be divided into two groups, Hagenianus and Gracilis. The species herein treated represent the entirety of the former group.

The common name usually applied to the members of the Hagenianus Group is "prairie crawfishes." This alludes to their distribution being principally in the prairie soils of eastern and central Mississippi and western Alabama. Although the type-locality is given as "Charleston, South Carolina," this surely is in error. Collections along the eastern seaboard have not revealed *P. hagenianus,* or even a near relative. The primary burrowing crawfishes *(sensu* Hobbs, 1942b) of the Charleston area are members of either *Cambarus* or *Fallicambarus* (Hobbs, 1972b).

In 1964 the collections on which Lyle had based his designations of the *nomina nuda* were located at Mississippi State University and transferred to the National Museum of Natural History. These specimens validated Lyle's contentions that there are several breeding populations of the taxon heretofore referred to as *Procambarus hagenianus* (Faxon). Fitzpatrick (1968) examined the Mississippi State University material and additional collections and discerned that each of Lyle's "subspecies" was a distinct taxon, and that two more taxa were represented. Following these morphological studies, the several populations were subjected to morphometric analysis and the parameters and limits of variation determined. This paper is a presentation of the results of those efforts.

During the course of these studies, the late Dr. Lyle was generous with his time and knowledge in helping me reconstitute the data on the collection and supplied many first-hand reminiscences of circumstances under which collecting was effected. Dr. Horton H. Hobbs, Jr., generously assisted via conversations, discussions, collecting and providing color photographs and field records. Drs. Horton H. Hobbs III, James F. Payne and Shih-ming Chien assisted in the field work, as did Messrs. Warren G. Anding and J. Paul Thaxton. The facilities of the National Museum of Natural History were made available on several visits. Randolph-Macon Woman's College, Lynchburg, Virginia, provided the time necessary for the mathematical computations on its Honeywell 1642 time-share digital computer. Ms. Barbara A. Laning provided clerical/technical assistance during much of the course of the study. The Research Committee of the University of South Alabama provided funds for preparation of the manuscript.

Specimens examined are designated as follows: Museum of Comparative Zoology (MCZ), National Museum of Natural History (USNM). Specimens not designated by a specific museum are in the collection of the writer, deposited at, but not yet catalogued by, the National Museum of Natural History, Smithsonian Institution.

The Hagenianus Group

Those members of the subgenus *Girardiella* Lyle of the genus *Procambarus* Ortmann which occur east of the Mississippi River flood plain were assigned to a newly created Hagenianus Group by Fitzpatrick (1975:384). He based his subdivision of the subgenus on morphological, geographic and evolutionary data. Because *P. hagenianus* is, by monotypy, the type of the subgenus *Girardiella,* the precise identity of this species is important. Hagen (1870) originally published figures and a description of a series which he called *Cambarus advena,* but Faxon (1884:140-141) tells us that the figures and descriptions were transposed with those of *C. carolinus,* according to Hagen's labels. Faxon then proceeded to rename Hagen's *carolinus* (described and figured as *advena) C. hagenianus.* For the identity of the several specimens called *advena*

by Hagen, see Hobbs (1974:47). Fortunately, however, the original description was based on a single specimen, which therefore becomes the type of the species and allows for precise definition. The matter is further complicated by the designated type-locality, Charleston, S.C. Animals compatible with the type do not occur within several hundred miles of Charleston. Hagen (1870:88) simply lists "Cat. 232, Charleston, S.C., Professor L. Gibbes. Male. Fem. / Spec. 2.", but Faxon (1914:366) adds that ". . . the type specimen . . . [was] received early in the history of the Museum [of Comparative Zoology, Harvard University] from Professor Lewis R. Gibbes of Charleston, S. C." Curatorial practices, even at leading museums, were not as stringent as they are today, and it was common for specimens received from a "cabinet," especially a famous one such as that of Professor Gibbes, to carry with them a locality designating the location of the cabinet rather than of the collection. Such seems to be the case with the type in question. The specimen probably was collected somewhere in the Black Belt of Alabama or Mississippi (see *"Range"* comments below).

Morphologically, the Hagenianus Group is distinct from the Gracilis Group which occurs west of the Mississippi River flood plain. In the Gracilis Group only *P. tulanei* Penn (1953) possesses a beard of plumose setae along the mesial margin of the palm of the cheliped in the Form I male; in the Hagenianus Group only *P. hagenianus (sens. str.)* lacks it. Another striking difference exists in the spinose ornamentation of the uropods. In the Hagenianus Group, all individuals bear two stout, acute spines on the mesial ramus of the uropod which project well beyond the distal margin of the ramus – one from the lateral corner and one from the median ridge. In *Procambarus* this characteristic is shared only with *P. (Acucauda) fitzpatricki* Hobbs (1971). The only other cambarid crawfish known to bear these spines with such a degree of development is *Fallicambarus (F.) macneesei* (Black, 1967) (Hobbs, 1973). Far more significant, however, are the differences in the first pleopods of Form I males. In all of the taxa of the Hagenianus Group a cephalic process is lacking, while this structure is present, albeit in varying degrees of development, in all members of the Gracilis Group. These differences are reflected in the structure of the pleopods of Form II males, but, in keeping with the usual lesser development of their secondary sexual characteristics, are less obvious.

MATERIALS AND METHODS

Each specimen was subjected to 10 measurements: (1) carapace length, (2) rostrum length, (3) rostrum width, (4) antennal scale length, (5) antennal scale width, (6) areola length, (7) chela length, (8) length of inner (= mesial) margin of palm, (9) palm width, and (10) dactyl length; in addition, in males pleopod length was measured. Techniques of measurement were those employed by Fitzpatrick (1967). For analyses of intra- and interspecific variability, appropriate ratios were calculated (except for carapace length), arcsine transformations performed, and the appropriate statistical procedures followed; additionally, the ratios were subjected to statistical analysis without transformation, and the results are presented graphically using Fitzpatrick's *(op. cit.)* method (Figs. 109-119).

Meristic and qualitative data were collected on the nature and quantity of setation on the inner margin of the palm and mesial margin of the dactyl, as well as the tubercular ornamentation of these structures. Similar data were collected for setation of the proximal podomeres of the third maxilliped. Data were accumulated concerning numbers and distribution of tubercular ornamentation on the opposable margins of the dactyl and immovable finger, and the standard morphological observations were made. Color notes and photographs were made on field collections by the writer, Hobbs, Jr., and Hobbs III; data made available by the latter two are incorporated where appropriate. Where notes were otherwise lacking, reference is made to Lyle's dissertation (1937) for color patterns.

In subsequent discussions, unless otherwise noted, all lengths are expressed as the ratio of carapace length to the specific measurement; consistently different are length of mesial margin of palm and dactyl length, both of which are expressed as ratios to chela length. Widths are expressed as ratios to the length of the particular structure.

Procambarus (Girardiella) hagenianus hagenianus (Faxon, 1884:141)

Figures 1-18

Cambarus advena. — Hagen, 1870:86, 87, figs. 90-92, (?)164; Fowler, 1912:567.

Cambarus Carolinus. — Hagen, 1870:31, 32, 53, 74, 75, 88 (part); Faxon, 1885:8, 9, 48, 54 (part), 55, 56, 58 (part), 65 (part), 158 (part), 167 (part), 173 (part).

Cambarus carolinus. — Brocchi, 1875:27; Faxon, 1884:140-141 (part); Ortmann, 1902:277, 279; Faxon, 1914:366; Hobbs and Villalobos, 1964:321, 322.

Cambarus Hagenianus. — Faxon, 1884:141; 1885:56.

Cambarus hagenianus. — Hay, 1902:38; Harris, 1903:58, 101, 137, 138, 154; Ortmann, 1905a:104; 1905b:438; Faxon, 1914:366-367, 412, Pl. I, Pl. VII: figs. 1, 7; Carr, 1936:1-11 (part); Lyle, 1938: 75; Hobbs, 1938:65; 1972a:7; Martin and Uhler, 1938:140; Hobbs and Villalobos, 1964:322; Fitzpatrick, 1975:381.

Cambarus (Cambarus) hagenianus. — Ortmann, 1905a:101.

Cambarus (Ortmannicus) hagenianus. — Fowler, 1912:341 (by implication). crawfish or crayfish. — Fisher, 1912:321-324, fig. 1 (probably *C. hagenianus* x *vesticeps).*

Cambarus (Girardiella) hagenianus hagenianus. — Lyle, 1938:76 (by implication).

Procambarus hagenianus. — Hobbs, 1942a:342 (by implication); 1942b:35, 71, 109; 1959:887; 1968:K9 (part); 1971:461, 466, 467; 1972a:4; Penn, 1953:166; Pennak, 1953:455; Smith, 1953:94; Fitzpatrick, 1968:37 (part); Dowell and Winier, 1970:489; Smiley and Miller, 1971:221; Momot and Gall, 1971:363; Payne, 1972:27; Hobbs and Bouchard, 1973:52; Reimer, 1975:25.

Procambarus (Girardiella) hagenianus. — Hobbs, 1972a:7, figs. 2d, 7a-g; 1972b:47 (part), 151 (part), 161 (part) (by implication), 162 (part) (by implication), figs. 21a, 39d, 40b; 1973:461; 1974:47 (part), fig. 192; Hobbs and Bouchard, 1973:63; Fitzpatrick, 1975:381, 382, 383, 384, 385, 387, 388.

Diagnosis. — Body pigmented, eyes small but well-developed. Rostrum (Fig. 5) with gently converging, rarely subparallel margins, lacking marginal spines; acumen short, indistinctly delimited basally. Areola 37.22-44.14% (avg. 42.00) of entire length of carapace; areola linear. Carapace devoid of cervical spines or tubercles. Suborbital angle absent, rarely obsolete (Fig. 11). Postorbital ridges lacking spines or tubercles cephalically. Cephalic portion of epistome (Fig. 18) subtrapezoidal in outline, usually with small cephalomedian tubercular projection. Antennal scale (Fig. 15) 1.59-3.31 (avg. 2.38) times longer than wide, widest distal to midlength, thickened lateral portion terminating distally in strong acute spine, which spine approximates 21% of entire length of scale. Mesial margin of palm (Fig. 14) devoid of conspicuous setiferous beard, instead with mesial row of 6-7 tubercles, and second row of 4-5 tubercles medial to it; upper and lower surface of palm covered with setiferous punctations; palm of female (Fig. 13) similar. Opposable margin of immovable finger with row of three small, one large and one small spine in proximal one-half, and crowded minute denticles in distal half, single ventromedially directed tubercle at base of distal one-fourth; opposable margin of movable finger slightly excavated in basal third, with two tubercles in excavation, middle one-third with row of one large, two small and one slightly removed small tubercle, crowded minute denticles in distal third and between penultimate and ultimate tubercle of margin. Ischia of third pereiopods only bearing hooks (Fig. 12); no prominences or bosses on coxae of third through fifth pereiopods. Mesial ramus of uropod (Fig. 16) with two conspicuous spines, median larger, projecting beyond distal margin. First pleopods (Figs. 1, 3, 4, 6, 7, 9, 10) symmetrical, shoulder present at base of central projection, pleopods reaching approximately to midlength of coxae of third pereiopods when abdomen flexed; distal extremity bearing (1) prominent acute mesial process directed caudodistally, extending beyond other terminal elements approximately by length of central projec-

tion, mesial process curving gently laterally in distal half; (2) well-developed central projection with apical portion bent laterally, centrocephalic process, centrocaudal process and mesial surface of mesial process enveloped at base by closely applied fold continuous with caudal surface of mesial process; and (3) conspicuous subrectangular (in lateral aspect) caudal process extending distally subparallel to central projection, caudodistal portion lamelliform; pleopods of second form male (Figs. 2, 8) less well developed and non-corneous. Annulus ventralis of female (Fig. 17) deeply excavate cephalomesially, with sulcus sloping precipitously toward cephalic margin, flanked laterally and/or cephalically by prominent ridges elevated (ventrally) two to three times height of remainder of annulus above sulcus, usually one cephalic and one lateral, each terminating in two or three tubercles; sinus originating in deep transverse fissure in cephalolateral quarter, running subparallel to longitudinal axis of animal to about middle of annulus, arcing sharply cephalomedially to approximately center then joining accessory sinus running from center of annulus to caudal one-fourth; postannular sternite subconical in shape.

Type. – MCZ no. 232. Male, Form I; by monotypy.

Type-locality. – Charleston, South Carolina. Clearly in error; see discussion above.

Range. – *P. hagenianus (sens. str.)* has been collected in association with the prairie soils, south and east of Tibbie Creek in the Tombigbee drainage of Lowndes, Noxubee and Oktibbeha counties, Mississippi, and Marengo, Pickens and Sumter counties, Alabama (Fig. 120). The easternmost and southernmost record is that given by Faxon (1914:366) as "Farmdale, Ala." (USNM no. 41462 and a derivative series, MCZ no. 7371). No record of such a town can be found, but a Faunsdale (Marengo County) does exist in the Black Belt. Considering that many labels were kept in script at that time, the emended spelling probably is correct. Specimens from the vicinity of Jackson, Mississippi (USNM no. 93101), probably represent mislabeled collections; this is discussed at greater length in the consideration of the range of *P. barbiger,* below. *The species does not exist in South Carolina.* The relationships of this race with a subspecies described below are discussed with the latter.

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Color. – As with all members of the Hagenianus Group, *P. hagenianus* is intensely colored and can be found in two color phases—one basically blue, the other basically red. Both phases, except for the base colors, are marked essentially the same. The blue phase is usually deep, nearly royal, blue, the intensity of which is accentuated by creamy-white rostral margins, postorbital ridges and often the finger tips. Lateral areas of the carapace are provided with a purplish blush which often extends onto a tan or reddish-brown abdomen. Hobbs, Jr., (personal communication) has provided me with his color notes of a red phase Form I male collected in Sumter County, Alabama. This is the most thorough description of a crawfish color I have seen, and he has generously given me permission to quote it as follows—

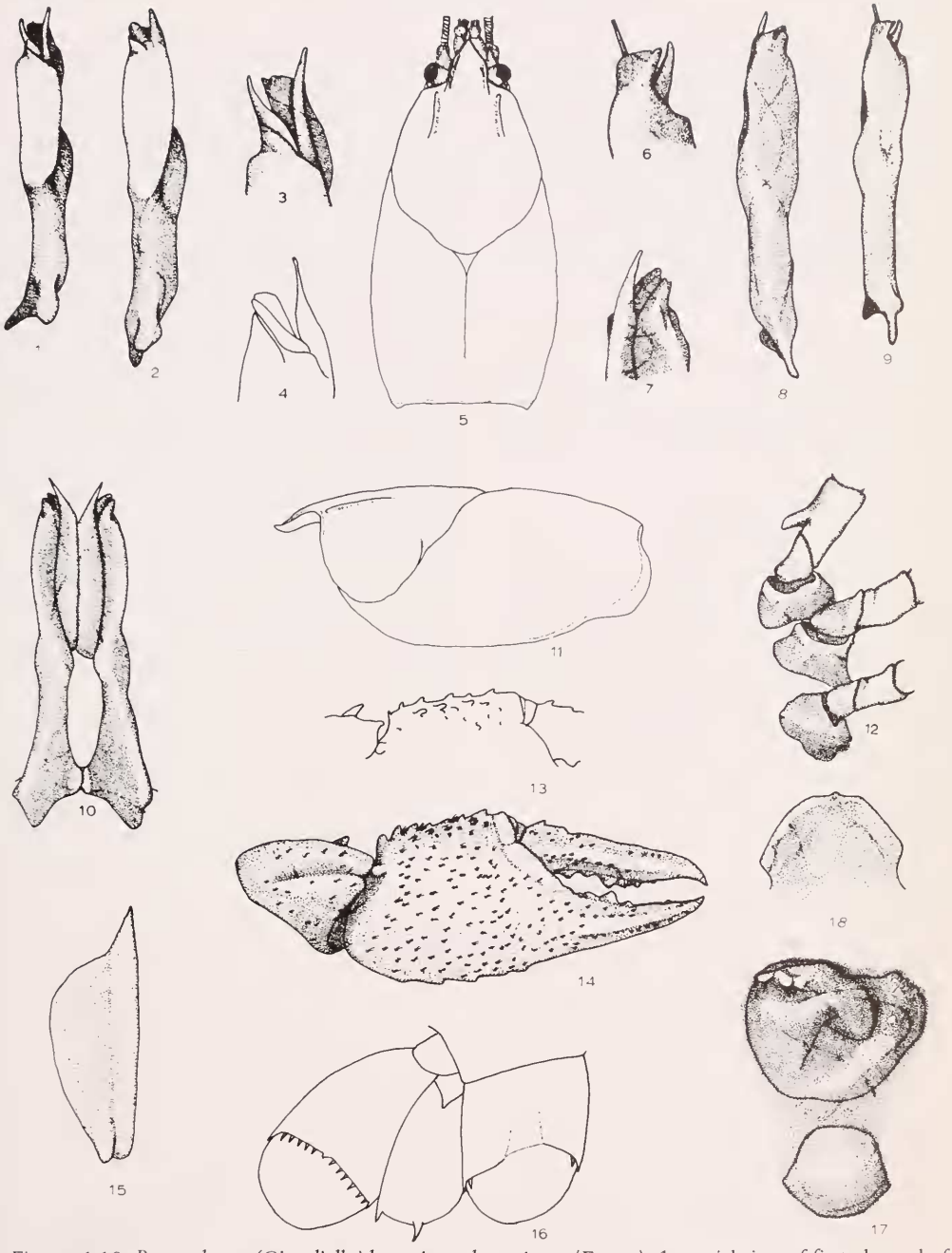
> "Cephalic section of carapace with rostral and postorbital ridges canary yellow to orange cream. Dorsum between ridges dark orange-tan. Dorsal part of hepatic region and area over mandibular muscle brick red; narrow reddish brown yoke, contiguous with cervical groove, joining caudal portions of red area across median line. Cream-tan arc extending from antennal region along and dorsal to cervical groove reaching level of cervical

tubercles. Tubercles in hepatic region tipped with cream to yellow. Cephalic triangular rudiment of areola reddish brown; branchiostegites olive with tan suffusion dorsolaterally and almost white laterally, part flanking cervical groove margined in orange cream dorsally and brick red laterally. First abdominal segment orange with pale markings on reduced pleura; cephalic segment of tergum of second segment with narrow dark red band; remainder of abdomen reddish brown dorsally with pleura brownish basally and almost cream marginally. Cephalic section of telson with paired brownish spots, remainder of tailfan orange tan flecked with brown. Eyestalks orange brown; peduncles of antennules and antennae mostly orange but with brown mottlings; flagella and antennal scale orange, tip of spine of latter pale pinkish cream. Cheliped basically orange with tan suffusion; spines on all podomeres and mesial row of tubercles on palm tipped with orange cream; tubercles on dorsal surface of palm and proximomesial surface of dactyl reddish brown. Remaining pereiopods and third maxillipeds orange with olive suffusion. Sternal areas pale orange to cream."

Variation. — Most of the variations encountered in this species are covered in the *"Diagnosis"* above or in the preceding discussion of color pattern. The usual variation of development of spinose and tubercular ornamentation is encountered, but I believe that the majority of such is the result of injury and/or wear and is not an inherent feature of the species. One often finds males, especially of Form I, in which the distal margin of the caudal process is sinuate or serrate, but this is due to in-life or *postmortem* breakage, as many specimens have a perfect margin on one pleopod and a sinuous or serrate margin on the other. This observation is valid for all members of the Hagenianus Group. Additionally, one should consider the variations noted for the subspecies following, especially the features seen in what I believe to be intergrades.

The results of morphometric analysis are as follows (based on 110 specimens: 54 ♂♂I, 9 ♂♂II, 47 ♀♀). Carapace length for Form I males was 23.9-39.0 (avg. 33.11), for females 27.8-40.4 (avg. 33.95) and for males, Form II, 25.5-32.7 (avg. 30.00). Form I males had a rostral length of 4.51-6.19 (avg. 5.14), females 4.16-5.82 (avg. 5.09) and Form II males 4.40-6.71 (avg. 5.22). The rostrum was 1.08-1.63 (avg. 1.40) times longer than wide in Form I males, 1.12-1.61 (avg. 1.36) times in females and 0.70-1.59 (avg. 1.36) in Form II males. Areola length was 2.27-2.69 (avg. 2.38) in Form I males, 2.30-2.53 (avg. 2.43) in females and 2.32-2.56 (avg. 2.44) in males, Form II. In Form I males antennal scale length was 6.53-9.52 (avg. 7.96), in females 6.08-9.13 (avg. 8.06) and 6.96-11.48 (avg. 8.67) in Form II males. Chela length in Form I males was 1.31-1.55 (avg. 1.41), in females 1.44-1.83 (avg. 1.61) and in Form II males 1.38-1.69 (avg. 1.53). Chela width was 2.03-2.53 (avg. 2.29) in Form I males, 2.01-2.43 (avg. 2.21) in females and 2.09-2.59 (avg. 2.36) in Form II males. Length of the inner margin of the palm was in Form I males 2.40-3.23 (avg. 2.82), 2.42-2.94 (avg. 2.67) in females and 2.56-2.97 (avg. 2.82) in Form II males. In males, Form I, dactyl length was 1.53-2.27 (avg. 1.67), in females 1.51-1.92 (avg. 1.72) and in Form II males 1.70-1.84 (avg. 1.76). Pleopod length was 2.88-4.05 (avg. 3.28) in Form I males and 3.21-5.43 (avg. 3.60) in Form II males. Table 2 gives the carapace length limits for all taxa.

Specimens examined. — ALABAMA: Marengo Co., Faunsdale (= "Farmdale"), 27 June 1910 (3 ♂♂I, 6 ♀♀), (1 ♂I, 1 ♂II, 1 ♀); Sumter Co., 2.8 mi. N of U.S. Hy. 11 on St. Rte. 39, along Jones Creek, 12 April 1974 (1 ♂I, 1 ♀ imm.); MISSISSIPPI: Hinds or Rankin Co., "near Jackson" (?), 6 May 1936 (2 ♂♂I, 1 ♂II, 16 ♀♀), (3 ♂♂I, 2 ♀♀); Lowndes Co., Mahew, 1 April 1936 (1 ♂I, 1 ♂II, 11 ♀♀), 4.5 mi W Columbus, 2 May 1936 (8 ♂♂I, 2 ♂♂II, 5 ♀♀); Noxubee Co., 6 mi E. of Macon, 6 March 1936 (11 ♂♂I, 5 ♂♂II, 6 ♀♀,1 ♀); Oktibbeha Co., Agricultural College (= Mississippi State University, = MSU), 11 and 13 March 1911 (1 ♂I, 9 ♀♀), 4 April 1911 (1 ♀), (1 ♂II, 11 ♀♀, 1 ♂imm., 1 ♀imm.), 11 May 1911 (2 ♀♀), 23 February 1912 (6 ♀♀), (6 ♀♀), 27 March 1916 (1 ♀), 1935 (17 ♀♀), Spring, 1936 (5 ♂♂I, 1 ♀), 26 April 1967 (1 ♂I, 2 ♀♀), 8 May 1967 (1 ♀), 7 April 1969 (1 ♀), (1 ♀), (1 ♀), (2



Figures 1-18. *Procambarus (Girardiella) hagenianus hagenianus* (Faxon): 1, mesial view of first pleopod of Form I male; 2, mesial view of first pleopod of Form II male; 3, terminal elements of first pleopod of Form I male, mesial view; 4, terminal elements of first pleopod of Form I male, cephalic view; 5, dorsal view of carapace of Form I male; 6, terminal elements of first pleopod of Form I male, lateral view; 7, terminal elements of first pleopod of Form I male, caudal view; 8, lateral view of first pleopod of Form II male; 9, lateral view of first pleopod of Form I male; 10 caudal view of first pleopods of Form I male; 11, lateral view of carapace of Form I male; 12, proximal podomeres of third through fifth pereiopods of Form I male; 13, mesial margin of palm of female; 14, distal podomeres of cheliped of Form I male; 15, antennal scale of male, Form I; 16, telson and left uropod of Form I male; 17, annulus ventralis and postannular sternite of female; 18, cephalic portion of epistome of Form I male.

♂♂ imm.), (1 ♀ imm.), (1 ♀), (1 ♀), no date (1 ♀), just SW of Starkville city limits, 7 July 1968 (1 ♂I, 1 ♀), 5 mi. N of Starkville, 1 April 1920 (1 ♂I, 2 ♀♀), Sand Creek, 11 May 1915 (2 ♂♂II, 3 ♀♀), about 10 mi. W of Columbus, April, 1948 (6 ♂♂I, 3 ♂♂II), (25 ♂♂I), "From hole near Chiltons" (Oktibbeha Co. ?), no date (4 ♂♂II, 9 ♀♀).

Procambarus (Girardiella) hagenianus vesticeps n. subsp.
Figures 19 - 36

Cambarus (Girardiella) hagenianus evansi Lyle, 1938:76, *nom. nud.*

Procambarus hagenianus. – Fitzpatrick, 1968:37 (part) (by implication).

Procambarus (Girardiella) hagenianus. – Hobbs, 1972b:47 (part), 151 (part), 154 (part) (by implication).

Procambarus (Girardiella) subsp. A. – Fitzpatrick, 1975:385, 386, 387, 388.

Diagnosis. – Body pigmented, eyes small but well-developed. Rostrum with gently converging margins, lacking marginal spines (Fig. 23); acumen short, indistinctly delimited basally. Areola 34.91-42.78 (avg. 39.85) % of entire length of carapace; areola linear. Carapace devoid of cervical spines or tubercles. Suborbital angle obsolete (Fig. 28). Postorbital ridges lacking spines or tubercles cephalically. Cephalic portion of epistome (Fig. 33) subovoid in outline, lacking cephalomedian tubercle. Antennal scale 2.11-2.94 (avg. 2.46) times longer than wide, widest distal to midlength, thickened lateral portion terminating in strong, but short, acute spine; mesiocephalic margin of lamellar portion with tubercular eminences from which tufts of setae protrude (Fig. 34). Mesial margin of palm (Fig. 32) with dense setiferous beard partially obscuring row of four or five tubercles; mesial margin of movable finger with small spinose tubercle in basal fourth, few setae emerging from distal base of tubercle. Opposable margin of immovable finger with row of two small, two large and one small tubercles in basal half, with crowded minute denticles in distal half, small ventromedially directed tubercle at base of distal fourth. Opposable margin of dactyl slightly excavated in basal third, with two small tubercles in excavation, one large and one small tubercle in remainder of basal half, crowded minute denticles along distal half. Ischia of third pereiopods only with spines; no prominences or bosses on coxae of third through fifth pereiopods (Fig. 31). Inner ramus of uropod with two conspicuous spines projecting beyond distal margin (Fig. 35). First pleopods (Fig. 19, 21, 22, 24, 25, 27, 29) slightly asymmetrical, strong right angular shoulder at base of central projection; pleopods reaching anterior margin of coxae of third pereiopods when abdomen flexed; distal extremity bearing (1) prominent subacute mesial process directed distally and subparallel to main axis of shaft; (2) well-developed central projection with apical portion bent slightly mesially and centrocephalic process enveloped at base mesially, cephalically and laterally by fold continuous with centro-caudal process laterally; and (3) conspicuous, well-developed, subrectangular (in lateral aspect) caudal process extending distally subparallel to central projection for 90% of length of central projection. Annulus ventralis of female deeply excavate cephalically, with strong cephalolateral and/or lateral ridges terminating (ventrally) in three or four tubercles, sinus originating at midlength of annulus in lateral fourth, running transversely to center of annulus then arcing gently to be lost in caudal margin of annulus; postannular sternite broadly conical in shape.

Holotypic male, Form I.—Body subovate, distinctly compressed. Abdomen narrower than thorax (9.3 and 12.6 mm). Width of carapace at caudodorsal margin of cervical groove less than height (12.6, 13.4 mm). Areola 41.58% of total length of carapace and linear; cephalic section of carapace 1.4 times length of areola (Fig. 23). Rostrum depressed (Fig. 28), deeply excavate dorsally, with thickened margins slightly converging cephalically, marginal spines lacking; acumen indistinctly delimited basally; upper surface sparsely punctate, but with usual submarginal row of setiferous punctations. Subrostral ridges moderately well developed to level just below suborbital angle and visible in dorsal aspect to about midlength of rostrum. Branchiostegal spine obsolete. Carapace punctate dorsally and laterally; granulate cephalolaterally with granules best

Table 1. Morphometric differences between Hagenianus Group crawfishes. Upper right half numbers are the numbers of characters in which there is at least 95% probability of difference; lower left half are the numbers in which the probability is 1% or less that there are no differences in the characters tested. Species abbreviations: BA = P. (G.) barbiger; CM = P. (G.) cometes; CN = P. (G.) connus; HH = P. (G.) h. hagenianus; HX = P. (G.) h. hagenianus X vesticeps; HV = P. (G.) h. vesticeps; PG = P. (G.) pogum.

		♂♂ I							♂♂ II						♀♀					
		BA	CM	CN	HH	HX	HV	PG	BA	CM	HH	HX	HV	PG	BA	CM	HH	HX	HV	PG
	BA	X	6	5	8	6	2	4			6	3	1		5	4	5	6	3	3
	CM	4	X	7	7	7	9	5			6	7	7	8	5	6	6	7	6	7
	CN	4	6	X	5	9	8	6			9	5	5	6	7	6	7	5	5	7
♂♂ I	HH	5	7	5	X	7	7	7			10	6	6	6	4	6	6	6	7	5
	HX	8	7	8	7	X	10	8			10	8	8	9	8	9	6	6	8	9
	HV	5	8	7	6	8	X	6			8	5	4	6	8	9	7	9	7	6
	PG	2	5	6	7	7	6	X			5	3	2	2	5	6	6	8	5	6
	BA								X											
	CM									X										
♂♂ II	HH	3	5	7	8	9	8	5			X	8	10	4	9	8	9	10	6	6
	HX	2	6	3	4	7	5	3			8	X	3	3	6	7	8	8	4	5
	HV	1	4	1	5	7	4	1			6	2	X	4	5	5	6	8	4	3
	PG	-	6	1	4	9	5	1			4	2	1	X	4	7	8	9	3	6
	BA	4	5	6	3	6	6	3			8	4	2	4	X	0	9	7	4	5
	CM	4	5	4	5	9	9	5			7	4	4	5	6	X	7	7	9	7
♀♀	HH	5	6	7	6	5	5	5			8	7	6	6	8	7	X	8	7	10
	HX	6	5	5	6	4	9	8			10	6	8	9	6	7	7	X	8	10
	HV	2	5	4	6	8	5	4			5	4	2	2	4	6	7	7	X	11
	PG	2	6	6	5	8	4	3			4	5	2	3	4	5	7	9	9	X

developed just posterior to suborbital angle. Cervical spines or tubercles absent. Cephalic section of telson (Fig. 35) with two spines in each caudolateral corner. Cephalic portion of epistome subovoid in outline, broader than wide, lacking cephalomedian tubercle. Antennules of usual form with well-developed spine on ventral surface of basal segment slightly distal to midlength. Antennae reaching to about caudal margin of carapace; antennal scale 2.4 times longer than wide, widest distal to midlength; thickened lateral portion terminating in strong acute spine approximately 13% of total length of scale.

Ischium of third maxilliped with long, stiff, dense setae arising from mesial margin and long but thinner and sparser tufts arising from ventrolateral margin.

Right chela with palm inflated, moderately depressed; lateral margin tubercular and nearly serrate; entire palmar area covered with setiferous punctations above and below; mesial margin of palm with mat of dense, long setae nearly obscuring mesial row of five strong tubercles, and row of four medial to it, setae arising in tufts from deep punctations; mesial margin of movable finger with two subequal tubercles in basal fourth, each with small tuft of coarse setae arising from cephalic margin, proximal one with tubercular eminence on upper margin. Opposable margin of immovable finger with row of three small, one large and two small tubercles in proximal half, distal half with crowded minute denticles and ventromedially directed tubercle at base of distal fourth; submedial longitudinal ridge above and below, both flanked by setiferous punctations. Opposable margin of movable finger excised in basal third and with two tubercles in excision, additionally one large and two small tubercles in basal two-thirds; distal third provided with crowded minute denticles; with submedian longitudinal ridge only moderately developed above and below, but both flanked with setiferous punctations.

Carpus of right cheliped longer than broad, with strong acute spine at base of distal third of mesial margin, three smaller spinose tubercles in proximal half, single spinose tubercle just distal to aforementioned strong spine; punctate above and below with submedian longitudinal furrow above; distal corners of ventral surface each with strong acute spine, row of two acute spines between ventral mesiodistal spine and strong spine of mesial margin.

Merus of right cheliped with single stout spine on distal dorsal margin and single tubercle just proximal to it; ventromesial margin with row of 13 acute subequal spines plus one strong acute spine distally; ventrolateral margin with row of five subequal acute spines. Ischium with mesial row of three spinose tubercles.

Hooks on ischia of third pereiopods only, directed proximally and extending over about distal third of basis. Coxae of third, fourth and fifth pereiopods lacking eminences or bosses.

First pleopods as described in *"Diagnosis"*; central projection and tip of caudal process corneous.

Uropods (Fig. 35) with mesial ramus bearing two stout subequal spines, one from lateral corner and one from medial ridge.

Sternites and coxae of third through fifth pereiopods bearing long (particularly on sternites) setae partially concealing pleopods when latter held under thorax. Measurements of all types of all taxa are given in Table 3.

Morphotypic male, Form II. – Differing from holotype in following respects: opposable margin of immovable finger bearing four small spines proximal to large spine and two distal to it in proximal half; opposable margin of movable finger with three tubercles (distalmost small) in excision and three tubercles distal to large tubercle; carpus lacking tubercles on mesial margin proximal to and just distal to stout spine. Terminal elements of first pleopod (Figs. 20, 26) less developed than holotype and parts noncorneous.

Allotypic female. – Differing from holotype in following respects: mesial margin of palm (Fig. 30) lacking dense beard, bearing instead three rows of setiferous tubercles, mesialmost row with six stout tubercles,

center row of six squamous tubercles and third row of four squamous tubercles in distal half of inner marginal area, all tubercles with tuft of setae emerging from distal base; upper surface of carpus with oblique row of four tubercles running proximodorsally from stout tubercle of mesial margin with additional two tubercles immediately dorsal to aforementioned stout spine.

Annulus ventralis (Fig 36) deeply excavate cephalomesially with sulcus falling precipitously from middle of annulus to cephalic margin, large cephalolateral and lateral ridges arising approximately twice depth of annulus (ventrally) above sulcus, left more laterally situated and terminating in three tubercles, right more cephalic and terminating in three tubercles, sinus originating in deep fissure at approximately midlength of annulus in right quadrant, running transversely to about center of annulus, then arcing gently sinistrad to be lost in caudal margin; postannular sternite broadly subconical in shape.

Types. – USNM nos. 146265, 146266, 146267 (holo-, allo-, and morphotype, respectively); *Paratypes:* Mississippi: Chickasaw Co. (12 ♂♂I, 2 ♂♂II, 5 ♀♀), Pontotoc Co. (1 ♀). Paratypes located at USNM.

Type-locality. – Egypt, Chickasaw Co., Mississippi.

Range. – This subspecies exists generally north of Tibbie Creek in the Tombigbee drainage of Chickasaw, Clay, Monroe and Pontotoc counties where it is apparently confined to the Black Belt of this area. The northernmost record is from "near Hurracine [*sic,* probably Hurricane; USNM no. 146275], near Thaxton." Southward it intergrades with the nominate subspecies, having an extensive hybrid population in and around Muldon (Monroe Co.). The characteristics of this intergrade population are discussed below under *"Variations."*

Color. – *P. hagenianus vesticeps* differs little in color from *P. h. hagenianus,* except that the colors are paler. I have never seen "red" individuals, but Lyle (1937) reports such. The color plates of Muldon specimens offered by Faxon (1914, Pl. 1) are good representations of the subspecies as I know it; Lyle *(op. cit.)* concurs.

Variations. – Based on morphometric analysis of 29 specimens (16 ♂♂I, 4 ♂♂II, 9 ♀♀). In most morphometric and gross morphological details *P. h. vesticeps* resembles the nominate subspecies. Carapace length for Form I males was 30.3-36.5 mm

TABLE 2. Size parameter ranges in Hagenianus Group crawfishes. All values are of carapace length in mm.

	♂♂I		♂♂II	♀♀
	Max.	Min.	Max.	Max.
P. (G.) h. hagenianus	39.0	23.9	32.7	40.4
P. (G.) h. vesticeps	36.5	30.3	37.9	40.0
P. (G.) h. hagenianus X vesticeps	42.8	27.6	39.0	40.4
P. (G.) barbiger	36.1	24.0		36.6
P. (G.) cometes	37.3	29.6		40.7
P. (G.) connus	41.0	26.6		
P. (G.) pogum	31.1	28.6	34.0	37.4

Table 3. Measurements (in mm) of type specimens of new species and subspecies. All appendages right, except asterisk (*) indicates left.

	Carapace			Rostrum		Areola	Ant. Scale		Cheliped			
	Length	Width	Height	Length	Width	Length	Length	Width	Length	Palm Width	Inn. Mar. Length	Dactyl Length
P. (G.) barbiger												
Holotype	36.1	16.1	19.0	8.0	6.2	15.3			24.1	10.6	8.6	14.5
Allotype	33.3	14.0	15.3	7.4	4.9	13.8			19.0	8.9	7.1	11.0
P. (G.) cometes												
Holotype	37.3	17.1	18.5	9.2	5.6	14.5	4.9	2.0	26.8	11.1	9.6	15.8
Allotype	31.8	13.3	13.7	8.0	4.8	10.5	3.8	1.4	16.7	7.3	6.0	10.7
Morphotype	31.6	13.2	14.7	7.0	5.1	12.9	4.0	1.8	20.2	8.5	7.5	11.2
P. (G.) connus												
Holotype	35.4	17.1	14.1	6.3	4.0	14.2	4.2	1.6	25.1*	10.1*	9.0*	13.7*
Allotype	35.2	15.4	13.8	6.4	5.1	14.7	4.2	1.6	22.1	9.8	8.2	12.2
Morphotype	29.0	14.1	11.7	5.6	4.4	11.5	3.2	1.3	19.9	9.0	7.5	11.0
P. (G.) pogum												
Holotype	28.6	14.1	14.5	8.5	4.8	11.0	4.1	1.5	18.9	12.9	5.5	12.0
Allotype	36.0	15.9	17.1	8.5	5.7	14.1	4.4	1.8	19.6	8.5	7.4	11.8
Morphotype	28.4	11.7	14.1	5.4	4.4	11.6	3.1	1.4	17.0	6.7	5.8	10.9
P. (G.) h. vesticeps												
Holotype	30.3	12.6	13.4	6.5	4.7	12.6	4.1	1.7	19.8	9.1	7.7	12.2
Allotype	35.4	15.0	15.7	7.6	5.6	14.8	4.7	1.8	21.6	9.3	8.3	12.2
Morphotype	36.0			7.7	5.8	15.4	4.0	1.8	16.7	11.4	10.0	15.6

(avg. 33.70), for females was 23.9-40.0 (avg. 33.23) and 23.2-37.9 (avg. 33.28) for Form II males. Form I males had a rostrum length of 4.44-5.56 (avg. 4.82), females 4.66-6.33 (avg. 5.23) and males, Form II, 4.57-4.93 (avg. 4.73); there was significant sexual dimorphism in this characteristic. The rostrum was 1.13-1.54 (avg. 1.36) times longer than wide in Form I males; 1.10-1.36 (avg. 1.27) in females and 1.28-1.46 (avg. 1.36) in Form II males. Areola length values for Form I males were 2.24-2.50 (avg. 2.40), 2.25-2.86 (avg. 2.45) for females and 2.34-2.86 (avg. 2.52) for Form II males. The antennal scale length for Form I males was 6.30-9.11 (avg. 8.03), for females 7.47-9.41 (avg. 8.35) and 7.73-9.00 (avg. 8.31) for Form II males. As expected, sexual dimorphism existed in the characteristics of the chela. Chela length in Form I males was 1.36-1.53 (avg. 1.41), in Form II males 1.38-2.16 (avg. 1.65) and in females 1.50-2.01 (avg. 1.76); chela width was 2.18-2.65 (avg. 2.31), 1.46-2.40 (avg. 2.08) and 2.07-2.88 (avg. 2.26), respectively. Form I males had an inner palm length of 2.48-2.82 (avg. 2.60) and a dactyl length of 1.62-1.83 (avg. 1.73). In Form II males the same values were, respectively, 1.67-2.84 (avg. 2.46) and 1.07-1.72 (avg. 1.46); and in females they were 2.42-2.73 (avg. 2.57) and 1.61-1.83 (avg. 1.74). Pleopod length in Form I males was 2.18-3.67 (avg. 3.35) and 3.27-3.67 (avg. 3.48) in Form II males.

Most morphological variations are within the limits set by the types, but some discussion of the populations around Muldon, Monroe County, Mississippi, seems necessary. This is the principal population on which I base my conclusion that *vesticeps* and *hagenianus* are conspecific, despite some striking morphological differences, most obvious of which are setiferous ornamentations. In one collection (USNM 57278, 2 ♂♂I, 5 ♀♀): all of the characteristics are of *vesticeps* except that the chelae are not bearded in one male, and the lateral margin of the ischium of the third maxilliped in all specimens is poorly provided with setae. In the females the postannular sternite is flat and trapezoidal in four and has a conical protuberance in the other. In one male the central projection is enveloped basally by a fold as in *hagenianus* on one pleopod, while on the other pleopod the composition is as in *vesticeps*. In USNM 44746, of 90+ specimens, there is one female with a postannular sternite and maxilliped setation intermediate between *hagenianus* and *vesticeps;* in two the sternite is *hagenianus*-like and the maxilliped is *vesticeps*-like; in nine the sternite-maxilliped characterizations are the reverse. Among the Form I males, seven have the setation of the ischium of the maxilliped and of the mesial margin of the hand much less dense than typical *vesticeps*. The remaining specimens are within the limits of variability typical of *vesticeps*. For morphometric comparisons a total of 130 specimens (55 ♂♂I, 4 ♂♂II, 71 ♀♀) of the intergrade population were used.

Specimens examined. – MISSISSIPPI: "NE Mississippi," 10 April 1911 (4 ♂♂I, 3 ♀♀); Chickasaw Co., Egypt, no date (6 ♂♂I, 3 ♂♂II, 6 ♀♀), Okalona (7 ♂♂I, 1 ♂II); Monroe Co., Slough at jct. St. Rtes. 8 and 25, 1 April 1966 (1 ♂ imm.); Pontotoc Co., "Nr. Hurracine [= Hurricane] nr. Thaxton," 1 May 1937 (1 ♀).

Intergrades *(P. h. hagenianus* x *P. h. vesticeps).* – MISSISSIPPI: Monroe Co., Muldon, July, 1912 (3 ♂♂I, 6 ♀♀), Fall, 1922 (1 ♂II, 6 ♀♀), no date (1 ♂I), (6 ♂♂I, 1 ♀), (1 ♂I, 1 ♀), (1 ♂I, 2 ♀♀); no locality, no date (♂♂I, ♂♂II, ♀♀, 90+ specimens).

Remarks. – Lyle (1937:44-45) reported: "The writer attempted to cross this crawfish [*C. h. evansi* (=*P. h. vesticeps*)] with *C. hagenianus* but was unable to get either species to mate in captivity." One must, however, consider this in light of the fact that *none* of his attempts at laboratory mating of *any* species was successful.

Etymology. – From *vesticeps* (L.): bearded, arrived at puberty; an allusion to the setiferous bearding characteristic of the hand and maxilliped in this subspecies.

Procambarus (Girardiella) barbiger n. sp.
Figures 37 - 52

Cambarus (Girardiella) hagenianus forrestae Lyle, 1938:76, *nom. nud.*

Procambarus hagenianus. – Fitzpatrick, 1968:37 (part).

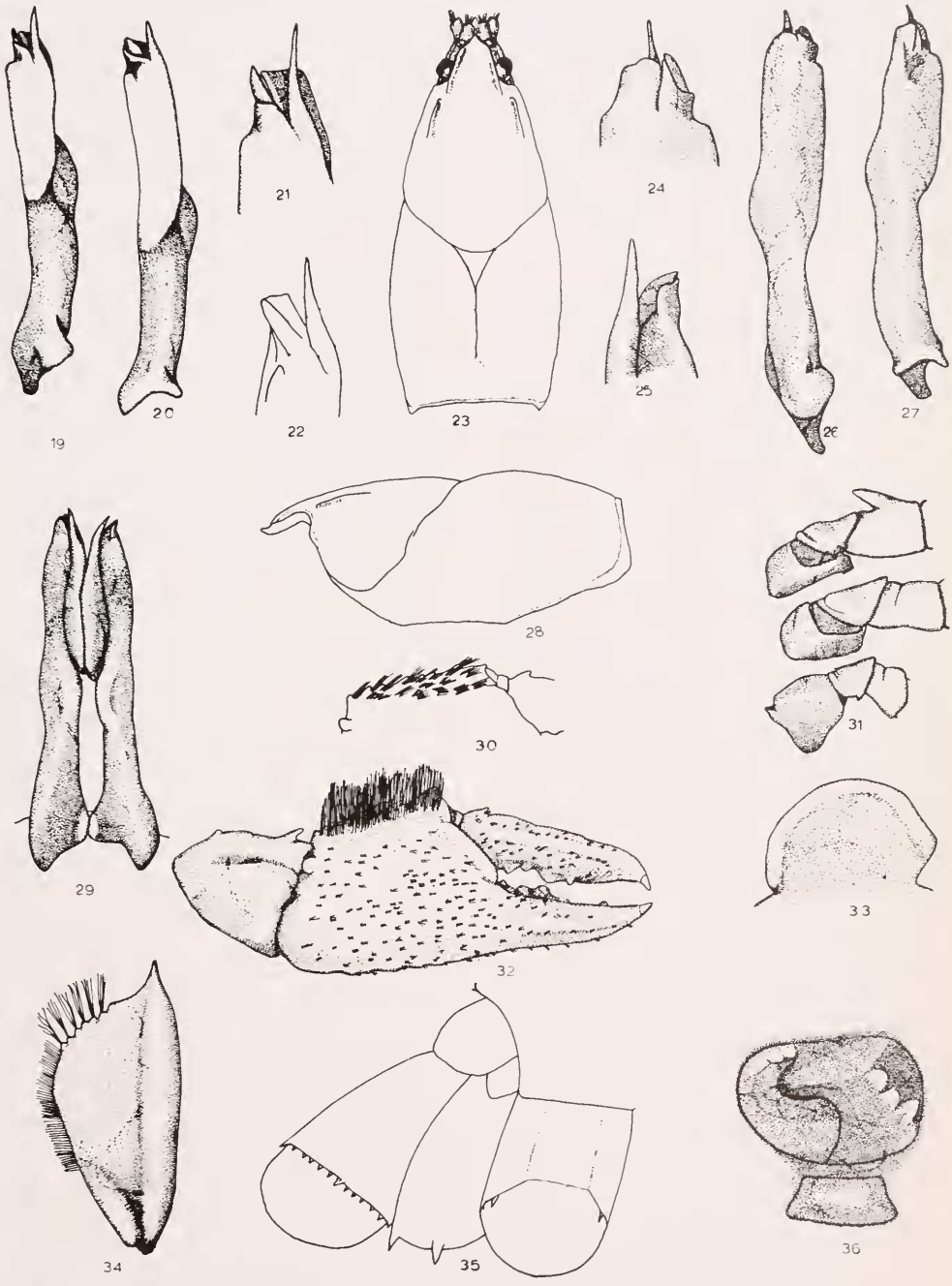
Procambarus (Girardiella) hagenianus. – Hobbs, 1972b:47 (part), 151 (part), 154 (part) (by implication).

Procambarus (Girardiella) sp. B. – Fitzpatrick, 1975:385, 386, 387, 388.

Diagnosis. – Body pigmented, eyes small but well-developed. Rostrum with gently converging margins, lacking marginal spines; acumen short, indistinctly delimited basally. Areola 38.32-43.87% of entire length of carapace (avg. 41.81); areola linear. Carapace devoid of cervical spines or tubercles. Suborbital angle obsolete. Postorbital ridges lacking spines or tubercles cephalically. Antennal scale 2.40-2.71 (avg. 2.69) times longer than wide, widest near midlength, thickened lateral portion terminating in strong, acute spine. Mesial margin of palm provided with dense setiferous beard, tubercles obscure; movable finger with small tuft of stout setae and strong tubercle distal to it on proximal fourth. Opposable margin of immovable finger with row of five prominent tubercles in proximal half, two in distal half, distal half with crowded minute denticles; opposable margin of movable finger with three stout tubercles, distal third with crowded minute denticles. Ischia of third pereiopods only with stout spine; no prominence or bosses on coxae of third through fifth pereiopods. Inner ramus of uropod with two conspicuous spines protruding beyond distal margin. First pleopods symmetrical, shoulder present at base of central projection; pleopods reaching caudal margin of coxae of third pereiopods when abdomen flexed; distal extremity bearing (1) prominent, subacute mesial process directed distally and slightly mesially, extending distally beyond other terminal elements; (2) well-developed central projection with apical portion bent slightly mesially, centrocephalic process enveloped at base by fold continuous with centro-caudal process; and (3) conspicuous, well-developed, subtriangular (in lateral aspect) caudal process extending distally subparallel to central projection for 80% of length of central projection, caudodistal margin lamelliform. Annulus ventralis of female very deeply excavate cephalically with strong cephalolateral ridges terminating (ventrally) in three to four tubercles and set off cephalically by groove; deep sinus originating in sulcus near center of annulus and describing gentle arc to caudal margin; postannular sternite in shape of triangular prism.

Holotypic male, Form I. – Body subovate, distinctly compressed. Abdomen narrower than thorax (11.6 and 16.1 mm). Width of carapace at caudodorsal margin of cervical groove less than height (16.1, 19.0 mm). Areola 42.38% of total length of carapace and linear; cephalic section of carapace 1.4 times as long as areola (Fig. 39). Rostrum sharply depressed (Fig. 43), deeply excavate dorsally, with thickened lateral margins slightly converging cephalically, marginal spines lacking, acumen indistinctly delimited basally; upper surface sparsely punctate, usual submarginal row of setiferous punctations present. Subrostral ridges moderately well-developed to level of suborbital angle and visible in dorsal aspect to midlength of rostrum. Branchiostegal spine small but acute. Carapace punctate dorsally and laterally; granulate cephalolaterally with granules best developed just posterior to suborbital angle. Cervical spines or tubercles absent. Cephalic section of telson with two spines in each caudolateral corner (Fig. 51). Cephalic portion of epistome subtriangular in outline, about as broad as long, lacking

Figures 19-36. *Procambarus (Girardiella) hagenianus vesticeps* n. subsp.: 19, mesial view of first pleopod of holotypic male, Form I; 20, mesial view of first pleopod of morphotypic male, Form II; 21, terminal elements of first pleopod of holotype, mesial view; 22, terminal elements of first pleopod of holotype, cephalic view; 23, dorsal view of carapace of holotype; 24, terminal elements of first pleopod of holotype, lateral view; 25, terminal elements of first pleopod of holotype, caudal view; 26, lateral view of first pleopod of morphotype; 27, lateral view of first pleopod of holotype; 28, lateral view of carapace of holotype; 29, caudal view of first pleopods of paratypic Form I male; 30, mesial margin of palm of allotype; 31, proximal podomeres of third through fifth pereiopods of holotype; 32, distal podomeres of cheliped of topoparatypic Form I male; 33, cephalic portion of epistome of holotype; 34, antennal scale of holotype; 35, telson and left uropod of holotype; 36, annulus ventralis and postannular sternite of allotype.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cephalomedian tubercle (Fig. 41). Antennules of usual form with well-developed spine on ventral surface of basal segment slightly distal to midlength. Antennae broken, but seemingly reaching to about caudal margin of carapace; antennal scale (Fig. 50) 2.4 times longer than wide, broadest approximately at midlength; thickened lateral portion terminating cephalically in strong acute spine about 18% of total length of scale.

Ischium of third maxilliped with long, stiff, dense setae arising from mesial and ventrolateral margins.

Right chela (Fig. 49) with palm inflated, moderately depressed; lateral margin nearly straight, not costate; entire palmar area covered with setiferous punctations; mesial margin of palm with mat of dense long setae obscuring tubercles; row of four squamous setiferous tubercles median to setal prominences; mesial margin of movable finger with tuft of setae in proximal fourth, prominent tubercle in proximal third distal to tuft of setae. Opposable margin of movable finger slightly excavate in basal third; with three stout tubercles in basal half, finger excavate in same region; three small tubercles distal to prominent tubercles and crowded minute denticles in distal fourth. Opposable margin of immovable finger with row of two small, one large, two small tubercles in basal half, one only in basal fourth; distal half with crowded minute denticles and with two small tubercles, one at origin of denticles, second halfway to tip. Both fingers with submedian longitudinal ridge above and below flanked by setiferous punctations. Lower surface of palm sparsely punctate with few tubercles in distal portion.

Carpus of right cheliped longer than broad with mesial margin bearing two strong spines near midlength and two spinose tubercles in mesiodistal fourth; punctate dorsally with longitudinal furrow slightly mesial to midline; lower distal margin with spine in each corner, third spine halfway between mesiodistal spine and aforementioned stout mesial spines.

Merus of right cheliped with dorsomedian row of 14 spines, distal three acute, remainder low and rounded, almost tubercular; ventral surface with mesial row of 11 irregularly spaced acute spines, stoutest distalmost, and lateral row of seven irregularly spaced spines, distalmost stoutest. Ischium with mesial row of two spines.

Hooks on ischia of third pereiopods only; hooks simple, directed proximally, projecting proximad to midlength of basis (Fig. 48). Coxae of third, fourth and fifth pereiopods lacking prominences or bosses.

First pleopods (Figs. 37, 38, 40, 42, 45, 47) as described in *"Diagnosis"*; central projection corneous.

Uropods (Fig. 51) with mesial ramus bearing two subequal spines projecting beyond caudal margin, one from lateral corner and one from median ridge. Sternites and coxae of all pereiopods, especially in pereiopodal segments II-V, bearing setae partially concealing pleopods when latter held under thorax.

Male, Form II. – Unknown.

Allotypic female. – Differing from holotype in following respects: areola 41.44% of entire carapace length; left antennal scale (Fig. 44) with two stout flat spines originating from middle of mesial margin of lamellar portion and mesiodistal margin of antennal scale. Mesial margin of palm (Fig. 46) with mesial row of seven setiferous squamous tubercles, row of six dorsomedial to them and irregularly spaced squamous setiferous tubercles over much of mesial half of upper surface; chelae proportionately shorter and less inflated; setiferous beard of ischia of third maxillipeds not as dense; pereiopodal sternites essentially lacking concealing setae.

Annulus ventralis (Fig. 52) deeply excavate cephalically with strong cephalolateral prominences extending (ventrally) one and one-half times depth of remainder of annulus, left terminating (ventrally) in two large and two small tubercles, right in three subequal tubercles; sinus originating near center of annulus, curving gently sinistrad to caudal margin; annulus delimited cephalically by groove. Postannular sternite as described in *"Diagnosis."*

Types. – USNM nos. 146258 (holotype) and 146259 (allotype); *Paratypes:* Missis-

sippi, Scott County (4 ♂♂I, 11 ♀♀).

Type-locality. – Forrest, Scott County, Mississippi.

Range. – This species is known only from burrows in and about Forrest, Scott Co., Mississippi, but probably occurs throughout the band of Jackson Prairie running southeastward from central Mississippi through Rankin, Scott, Smith, Newton, Jasper, Clarke and Wayne counties and possibly Madison and Hinds counties. All of the known specimens were collected from the environs of Forrest, and I have never been able to collect the species personally despite repeated efforts. I have, however, attempted the excavation of burrows which were probably made by this species near Forrest, and the environmental situation in which these burrows occurred was nearly identical with that in which *P. hagenianus* is found– large open fields relatively remote from watercourses. Lyle (1937:48) recorded the species (as *P. h. forrestae)* from "Leesburg, Rankin County," but I have been unable to locate the specimens on which this record is based. The only "Rankin" specimens I have seen are USNM no. 93101 ("near Jackson [Hinds or Rankin Co.], leg. Carlysle Carr, May, 1936") which are unquestionably assignable to *P. h. hagenianus.* Mr. Carr, an employee of the U. S. Biological Survey, worked intimately with the state Fish and Wildlife Service, and I believe that the locality appearing on the label of these specimens reflects that the specimens were received from Jackson, on the site of the Fish and Wildlife Service Museum. I offer in support of this thesis the fact that no other specimens resembling the subspecies have been collected or reported from the vicinity of Jackson.

Color. – I have never seen fresh specimens personally, but Lyle (1937:48) gives a limited description: "color is rather variable but blue apparently predominates."

Variation. – Most of the limits of variation are within the limits set by the primary types, but in a collection of two females (USNM no. 146273) one specimen is typical of *barbiger,* and the other lacks the hirsute ornamentation of the mesial portion of the palm; furthermore the annulus is not typical. Neither specimen possesses the lateral row of dense setae on the ischium of the third maxilliped, but both have a postannular sternite characteristic of *barbiger.* In the topotypic series (4 ♂♂I, 9 ♀♀), one female has a dextrally oriented sinus and less prominent tubercles on the annulus than the rest of the specimens; in another female the tubercles are placed much more cephalomesially than the rest; in a third specimen the tubercles are broad, prominent and lateral; and in a fourth the tubercular prominences seem almost montane in comparison. The shoulder on the cephalic surface of the first pleopod of one male is much more sharply angular than in the remaining specimens.

Morphometric analysis was based on 15 specimens (4 ♂♂I, 11 ♀♀). Carapace length was 24.0-36.1 (avg. 29.15) in Form I males and 28.5-36.3 (avg. 32.17) in females. In males, Form I, rostrum length was 3.87-4.51 (avg. 4.27) and 4.16-5.00 (avg. 4.48) in females. The rostrum was 1.29-1.55 (avg. 1.45) times longer than wide in Form I males and 1.16-1.76 (avg. 1.43) in females. The areola length was 2.36-2.43 (avg. 2.39) in Form I males and 1.77-2.61 (avg. 2.42) in females. Antennal scale values were available only for females, and they were 7.68-7.80 (avg. 7.74) for length and 2.67-2.71 (avg. 2.69) for width. Chela length was 1.47-1.50 (avg. 1.48) in Form I males and 1.69-1.84 (avg. 1.77) in females. Chela width was 2.17-2.40 (avg. 2.28) in Form I males and 2.03-2.15 (avg. 2.09) in females. In Form I males length of the mesial margin of the palm and dactyl length were, respectively, 2.67-2.80 (avg. 2.75) and 1.66-1.72 (avg. 1.69), while the same two characters in females were 2.06-2.68 (avg. 2.46) and 1.61-1.73 (avg. 1.67). Pleopod length in the Form I males was 3.08-3.84 (avg. 3.44).

Specimens examined. – MISSISSIPPI: Scott Co., Forrest, 2 May 1936 (4 ♂♂I, 9 ♀♀), March, 1934 (2 ♀♀).

Remarks. – In the topotypic series, collected 2 May 1936, three of the nine females had a sperm plug in the annulus ventralis.

Etymology. – From *barbiger* (L.): wearing a beard; so named because of the hirsute

nature of the mesial margin of the hand in both sexes and the bearding of the ischium of the third maxilliped.

Procambarus (Girardiella) cometes n. sp.
Figures 53 - 71

Procambarus (Girardiella) hagenianus. – Hobbs, 1972b:47 (part), 151 (part), 154 (part) (by implication).

Procambarus (Girardiella) sp. E. – Fitzpatrick, 1975:385, 386, 387, 388.

Diagnosis. – Body pigmented, eyes small but well-developed. Rostrum with slightly converging margins, lacking marginal spines; acumen short and indistinctly delimited basally. Areola linear and 38.77-43.24 (avg. 40.01)% of total length of carapace. Carapace devoid of cervical spines or tubercles. Suborbital angle absent. Postorbital ridges without spines or tubercles. Antennal scale 2.33-2.87 (avg. 2.51) times longer than wide, broadest near midlength, thickened lateral portion terminating cephalically in long, acute, stout spine. Mesial margin of palm with surface obscured by dense mat of setae in first form male, second form male with numerous tufts of short stiff setiferous bristles, female with single row of five or six tubercles and sparse setiferous squamous tubercles; basal portion of movable finger excavate along opposable margin with row of five or six tubercles in basal two-thirds; opposable margin of immovable finger with row of seven or eight tubercles in basal two-thirds and single tubercle at base of distal fourth. Ischia of third pereiopods only bearing simple hooks; coxae of third, fourth and fifth pereiopods lacking prominences or bosses. Inner ramus of uropod with two conspicuous spines projecting distally beyond margin. First pleopods symmetrical, reaching caudal margin of coxa of third pereiopod when abdomen flexed; small shoulder present at base of central projection; distal extremity bearing (1) prominent central projection directed more or less laterodistally (2) subacute mesial process directed laterodistally, projecting only slightly beyond tips of other elements; and (3) subrhomboidal (in lateral aspect) caudal process excavate mesially, lamelliform in caudodistal half. Annulus ventralis of female deeply excavate cephalically with prominent cephalolateral ridges terminating (ventrally) in tubercles, sulcus relatively narrow (only 20-25% width of annulus), annulus set off cephalically by shallow groove; sinus originating near center of annulus and passing in gentle arc to caudal margin; postannular sternite subconical in shape.

Holotypic male, Form I. – Body subovate, distinctly compressed. Abdomen narrower than carapace (13.3 and 17.1 mm). Carapace higher than wide at caudodorsal margin of cervical groove (18.5, 17.1 mm). Areola 38.87% of total length of carapace and linear (Fig. 57). Cephalic section of carapace 1.6 times as long as areola. Rostrum slightly depressed (Fig. 62), deeply excavate dorsally with thickened lateral margins gently convergent distally, marginal spines lacking, acumen indistinctly delimited basally; upper surface sparsely punctate, usual row of submarginal setiferous punctations present. Subrostral ridges moderately well-developed from suborbital level and visible to about midlength of rostrum in dorsal aspect. Postorbital ridges moderately prominent, grooved dorsolaterally, and terminating cephalically without spines or tubercles. Suborbital angle lacking. Branchiostegal spine reduced. Carapace very sparsely punctate but with squamous tubercules laterally, tubercles most numerous in cephaloventral portion. Cervical spines or tubercles absent. Telson (Fig. 70) divided with two spines in right caudolateral corner and three in left. Cephalic portion of epistome (Fig. 68) about as broad as long with tubercular mesiocephalic projection. Antennules of usual form with well-developed spine on ventral surface of basal segment slightly distal to midlength. Antennae extending about to caudal margin of carapace; antennal scale (Fig. 69) 1.57 times longer than wide, broadest distal to midlength, thickened lateral portion terminating cephalically in strong acute spine approximately 23% of total length of antennal scale, cephalic margin of lamellar portion provided with relatively few tubercular eminences bearing tufts of setae.

Ischium of third maxilliped with prominent, stiff, simple, unmatted setae running along entire mesial and ventrolateral margin.

Right chela (Fig. 67) with palm inflated, not strongly depressed; lateral margin not costate; upper and lower surfaces punctate except along mesial margin; mesial margin of palm almost devoid of tubercles but provided with dense mat of long, stiff setae; setae in distinct tufts arising from large, deep punctations. Opposable margin of fixed finger with row of three small, one large, and three small tubercles in basal two-thirds, single large tubercle directed ventromesially from base of distal fourth, distalmost 10% broken, but with crowded minute denticles distal from tubercle; submedian longitudinal ridge flanked by setiferous punctations above. Opposable margin of dactyl excavate in basal half with row of three small, one large and two small tubercles along basal two-thirds, crowded minute denticles in distal fourth; mesial margin with two evenly spaced setiferous tubercles in basal fourth; submedian longitudinal ridge above flanked by setiferous punctations.

Carpus of right cheliped longer than wide, with mesial margin bearing stout acute spine in distal fourth, small acute spine in mesiodistal corner; remainder of upper surface punctate, but with longitudinal furrow in distalmost three-fourths; lower surface with strong acute spines in each distalmost corner. Merus of right cheliped with row of ten tubercles on upper surface and two acute spines terminating row distally; lower surface with mesial row of 14 acute spines increasing in size distally, and lateral row of nine smaller acute spines likewise increasing in size distally. Ischium with mesial row of two small tubercles.

Hooks on ischia of third pereiopods only (Fig. 65); hooks simple, directed proximally and projecting proximally to distal fourth of basis. Coxae of third, fourth and fifth pereiopods lacking prominences or bosses.

First pleopods symmetrical and as described in *"Diagnosis"*; central projection and caudal process corneous (Fig. 53, 55, 56, 58, 59, 61, 66).

Uropods (Fig. 70) with mesial ramus bearing two spines projecting beyond caudal margin, one from lateral corner, and other, slightly longer, from median ridge.

Sternum between coxae of second through fifth pereiopodal segments slightly excavate, lateral margins bearing sparse tufts of setae only partially obscuring first pair of pleopods when pleopods held beneath thorax.

Morphotypic male, Form II. – Differing from holotype in following respects: dorsal punctation of carapace present; tip of immovable finger of chela unbroken and crowded minute denticles occurring to level of corneous acute tip; mesial margin of palm (Fig. 63) lacking dense bearding, but provided with numerous tufts of shorter setae clearly arising from deep large setiferous punctations; carpus of cheliped bearing small acute spine between mesial spine and ventromesial spine on both chelipeds. First pleopods (Figs. 54, 60) with tips non-corneous, proportionally less developed, and central projection with fold at base wrapping around mesial, cephalic and lateral portions, mesial process extending proportionately farther beyond tip of other elements. Only two spines in left caudolateral margin of cephalic portion of telson. Hooks on ischia of third pereiopods much less pronounced than in holotype.

Allotypic female. – Differing from holotype in following respects: cephalic portion of epistome subtrapezoidal and broader than long; areolar region with transverse crease *pre-mortem* injury and only 33.02% of total length of carapace; mesial margin of chela (Fig. 64) lacking beard, bearing instead five tubercles, some of which provided with quite light setiferous tufts; distalmost portion of immovable finger similar to that of morphotype; small acute spine between spine and ventrodistal spine of carpus as in morphotype.

Annulus ventralis (Fig. 71) about as broad as long, with deep subtrapezoidal excavation in centrocephalic portion, cephalolateral margins markedly raised (ventrally) with three tubercles on left ventralmost margin and four on right; sinus originating near center, forming arc sinistrally and be-

coming lost in caudal margin near midline; postannular sternite subconical in shape.

Types. – USNM nos. 130227, 146260, and 131280 (holo-, allo-, and morphotype, respectively); *Paratypes:* Oktibbeha (2 ♂♂I, 9 ♀♀) and Lowndes (1 ♂I) counties, Mississippi.

Type-locality. – Field behind Luxury Mobile Homes (T18N, R14E, SW¼, Sec. 3), Starkville, Oktibbeha County, Mississippi.

Range. – The species is known from only two localities in Oktibbeha County (the type locality and 8.8 mi S of Starkville, jct. St. Rte. 25, on St. Rte. 12) and one in Lowndes County (6.6 mi E of Old State Route 12 in Starkville). It seems to be associated with the Flatwoods belt in Oktibbeha Co., but the specimen from Lowndes Co. came from the Black Belt.

Color. – *P. cometes* resembles *P. hageni-anus* in color–dark blue ground color with cream markings–but I have never seen a "red" phase. This species was unknown to Lyle, therefore he left no color notes.

Variation. – Most of the limits of variation are incorporated in the diagnosis and descriptions above. In four female specimens from south of Starkville (USNM no. 146274), the mesial margin of the hands is provided with sparse, widely scattered tufts of setae not markedly different from the condition found in *P. barbiger;* an associated Form I male is typical of the species. The extremely short areola (comparatively) of the allotype seems to be unique.

Morphometric variation analysis is based on 14 specimens (4 ♂♂I, 10 ♀♀). Carapace length in males was 29.6-37.3 (avg. 33.30) and 31.8-40.7 (avg. 35.54) in females. In males the rostrum length was 4.05-4.63 (avg. 4.24) and in females 3.98-4.69 (avg. 4.35), while rostrum width values were 1.33-1.66 (avg. 1.54) and 1.34-1.67 (avg. 1.46), respectively. Areola length was 2.45-2.58 (avg. 2.54) in males and 2.31-3.03 (avg. 2.54) in females. Antennal scale length was 7.65-8.05 (avg. 7.75) in males and 7.39-8.85 (avg. 8.12) in females. Chela length in males was 1.39-1.66 (avg. 1.51) and in females was 1.71-1.92 (avg. 1.81); chela width was 2.23-2.46 (avg. 2.34) in males and 2.05-2.47 (avg. 2.26) in females. Length of the mesial margin of the palm and length of the dactyl were, respectively, in males 2.79-2.97 (avg. 2.88) and 1.52-1.70 (avg. 1.64); in females the same characters in the same sequence were 2.59-3.01 (avg. 2.77) and 1.56-1.90 (avg. 1.66). Pleopod length in males was 3.65-3.89 (avg. 3.72).

Specimens examined. – MISSISSIPPI: Lowndes Co., 6.6 mi. E of Starkville, 12 July 1968 (1 ♂I); Oktibbeha Co., Luxury Mobile Homes (T18N, R14E, SW¼ Sec. 3), Starkville, no date (1 ♀), (1 ♂I, 1 ♀), (1 ♂I), (1 ♀), (3 ♀♀), 8.8 mi. S of Starkville on St. Rte. 12, no date (1 ♂I, 4 ♀♀).

Etymology. – From *cometes* (L.): one with long hair; used with reference to the long setae on the mesial margin of the palm of males and the long setae on the ischium of the third maxilliped.

Procambarus (Girardiella) connus n. sp.
Figures 72 - 90

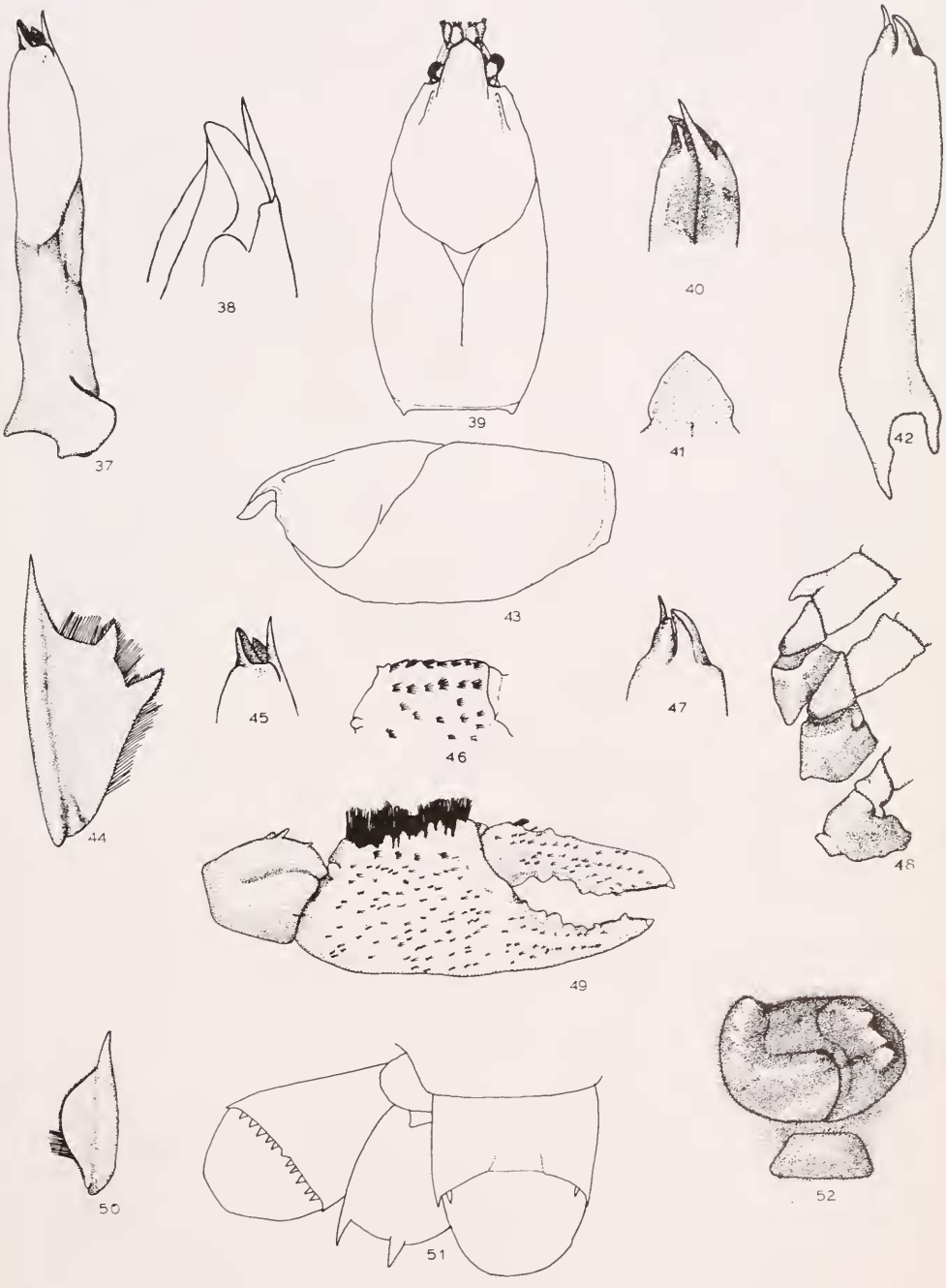
Procambarus hagenianus. – Fitzpatrick, 1968:37 (part).

Procambarus (Girardiella) hagenianus. – Hobbs, 1972b:47 (part), 151 (part), 154 (part) (by implication).

Procambarus (Girardiella) sp. C. – Fitzpatrick, 1975:385, 386, 387, 388.

Diagnosis. – Body pigmented, eyes small but well-developed. Rostrum with gently

Figures 37-52. *Procambarus (Girardiella) barbiger* n. sp.: 37, mesial view of first pleopod of holotypic male, Form I; 38, teminal elements of first pleopod of holotype, cephalic view; 39, dorsal view of carapace of holotype; 40, terminal elements of first pleopod of holotype, caudal view; 41, cephalic portion of epistome of holotype; 42, lateral view of first pleopod of holotype; 43, lateral view of carapace of holotype; 44, left antennal scale of paratypic female; 45, terminal elements of first pleopod of holotype, mesial view; 46, mesial margin of palm of allotype; 47, terminal elements of first pleopod of holotype, lateral view; 48, proximal podomeres of third through fifth pereiopods of holotype; 49, distal podomeres of cheliped of holotype; 50, antennal scale of holotype; 51, telson and left uropod of holotype; 52, annulus ventralis and postannular sternite of allotype.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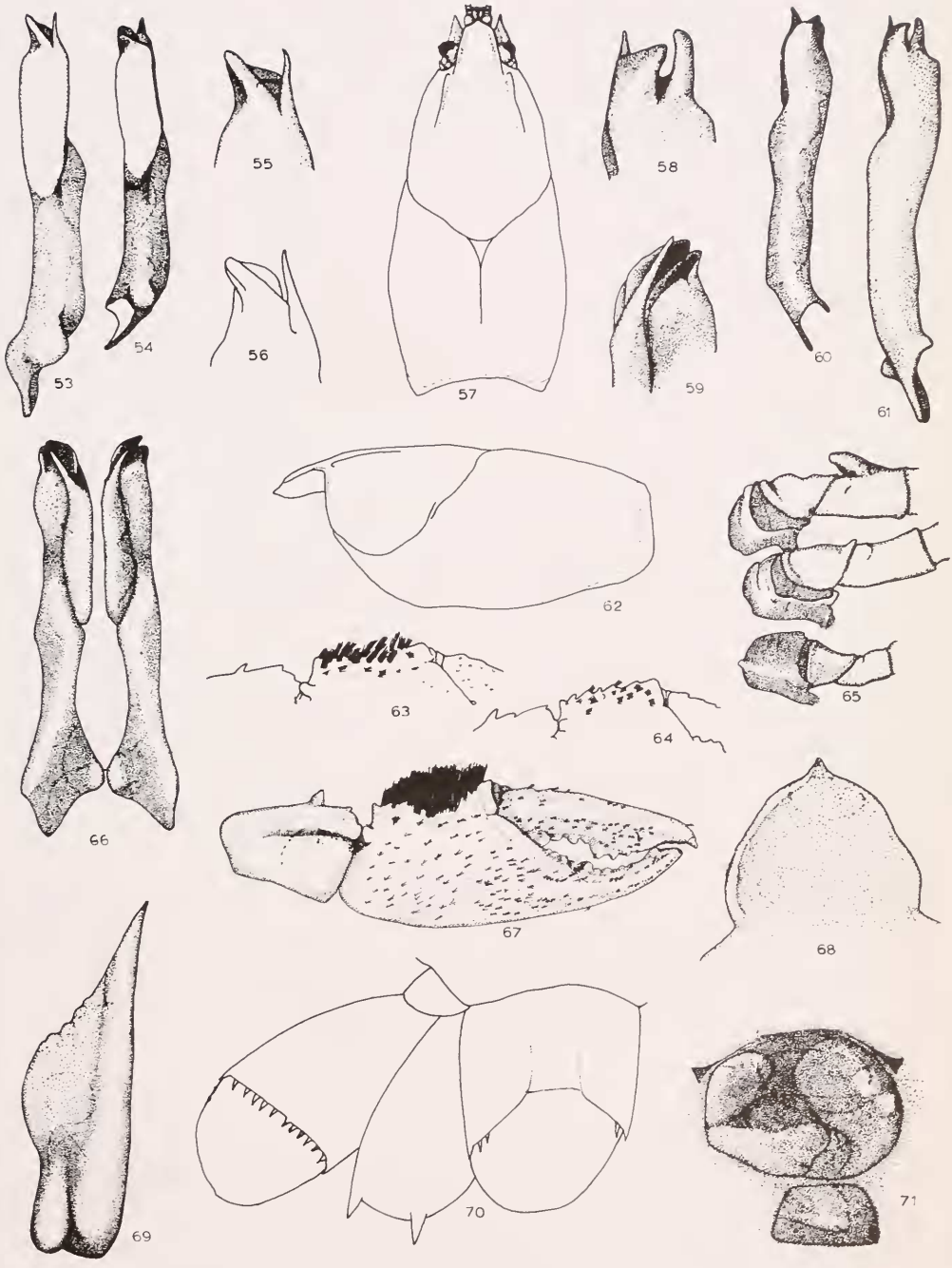
converging margins, lacking marginal spines, acumen short and indistinctly delimited basally. Areola constituting 38.39-44.79 (avg. 41.41)% of total length of carapace; areola linear. Carapace devoid of cervical spines or tubercles. Suborbital angle obsolete. Postorbital ridges without spines or tubercles. Antennal scale 2.00-2.88 (avg. 2.44) times longer than wide, thickened lateral portion terminating cephalically in stout, comparatively short spine, broadest slightly distal to midlength. Mesial margin of palm with setiferous mat of hairs obscuring tubercular ornamentation. Opposable margin of immovable finger with row of eight tubercles in basal three-fourths, third from base largest; opposable margin of dactyl slightly excavated in basal third, with row of seven tubercles, first and fourth larger than remainder. Ischia of third pereiopods only bearing simple hooks; coxae of third, fourth and fifth pereiopods lacking prominences or bosses. Inner ramus of uropod with two conspicuous spines projecting distally beyond margin. First pleopods very slightly asymmetrical, slight shoulder at base of central projection; distal extremity bearing (1) prominent central projection directed laterodistally, tightly applied fold continuous with centrocaudal process enveloping base of centro-cephalic process; (2) subacute mesial process directed caudal subparallel to main axis of shaft, extending length of central projection beyond other terminal elements; and (3) subrectangular (in lateral aspect) caudal process subparallel to mesial plane of pleopod with caudodistal margin lamelliform. Female with rather simple (in comparison with relatives) annulus ventralis; annulus deeply excavate in centrocephalic portion with prominent lateral prominences (ventrally), prominences lacking tubercular ornamentation; annulus set off cephalically by groove; sinus originating slightly anterior to center of structure, curving sinistrally to be lost in caudal fourth; postannular sternite subrhomboid in outline, not highly elevated.

Holotypic male, Form I. — Body subovate, distinctly compressed. Abdomen narrower than carapace (10.3 and 17.1 mm). Width of carapace at caudodorsal margin of cervical groove greater than height (17.1, 14.1 mm). Areola 41.24% of total length of carapace; areola linear (Fig. 76). Cephalic section of carapace 1.4 times as long as areola; rostrum depressed, deeply excavated dorsally, with gently converging thickened lateral margins, marginal spines lacking, acumen indistinctly delimited basally; upper surface not punctate except for usual submarginal row of setiferous punctations. Subrostral ridges moderately well-developed from level of suborbital angle and visible dorsally to approximately midlength of rostrum. Postorbital ridges moderately well developed, grooved cephalolaterally, terminating cephalically without spines or tubercles. Suborbital angle obsolete (Fig. 81). Branchiostegal spine small, but acute. Carapace very sparsely punctate dorsally but with squamous tubercles on cephalolateral portion. Cervical spines or tubercles absent. Cephalic section of telson (Fig. 88) with three spines in right caudolateral corner and two in left. Cephalic portion of epistome (Fig. 90) subovate in outline, lacking tuber-

Figures 53-71. *Procambarus (Girardiella) cometes* n. sp.: 53, mesial view of first pleopod of holotypic male, Form I; 54, mesial view of first pleopod of morphotypic male, Form II; 55, terminal elements of first pleopod of holotype, mesial view; 56, terminal elements of first pleopod of holotype, cephalic view; 57, dorsal view of carapace of holotype; 58, terminal elements of first pleopod of holotype, lateral view; 59, terminal elements of first pleopod of holotype, caudal view; 60, lateral view of first pleopod of morphotype; 61, lateral view of first pleopod of holotype; 62, lateral view of carapace of holotype; 63, mesial margin of palm of morphotype; 64, mesial margin of palm of allotype; 65, proximal podomeres of third through fifth pereiopods of holotype; 66, caudal view of first pleopods of holotype; 67, distal podomeres of cheliped of holotype; 68, cephalic portion of epistome of holotype; 69, antennal scale of holotype; 70, telson and left uropod of holotype; 71, annulus ventralis and postannular sternite of allotype.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cular median protrusion. Antennules of usual form with well-developed spine on ventral surface of basal segment slightly distal to midlength. Antennae extending caudad approximately to caudal margin of carapace. Antennal scale (Fig. 83) 2.07 times longer than wide, widest slightly distal to midlength, thickened lateral portion terminating cephalically in very stout spine approximately 21% of total length of antennal scale; cephalic half of margin of mesial lamellar portion provided with numerous tubercular eminences bearing tufts of setae.

Ischium of third maxilliped with prominent simple, stiff, unmatted setae along mesial and ventrolateral margins.

Right chela (Fig. 85) with palm inflated, not strongly depressed; lateral margin not costate; entire palmar area covered with setiferous punctations; mesial margin with row of five prominent tubercles and second row of four above, both rows nearly obscured by beard of setae in tufts arising from deep punctations. Opposable margin of immovable finger excavate in basal third; with row of three small, one large and three small tubercles in basal two-thirds, another tubercle at level of basal fourth, except for aforementioned tubercle distal one-third with crowded minute denticles; finger with submedian longitudinal ridge above and below, both flanked by setiferous punctations. Opposable margin of dactyl with row of one large, two small, one large and three small tubercles in basal two-thirds, with crowded minute denticles beginning just distal to penultimate tubercle and extending to tip of finger, slightly excavate in proximal third; mesial margin with two tubercles in basal one-fourth (distalmost largest); submedian longitudinal ridge above, and less distinct one below, both flanked by setiferous punctations.

Carpus of right cheliped longer than broad; with mesial margin bearing stout acute spine at base of distal third, two small but acute spines, equally spaced, proximal to aforementioned spine, upper mesiodistal margin and corner with three small spines; longitudinal groove above; small acute spine in each ventrodistal corner with row of two acute spines between mesiodistal spine and stout spine of medial surface.

Merus of right cheliped with two stout spines on upper surface near distal margin; mesioventral margin with row of 12 acute spines, distalmost largest, and ventrolateral margin with row of six, increasing in size distally. Ischium with mesial row of three acute spines.

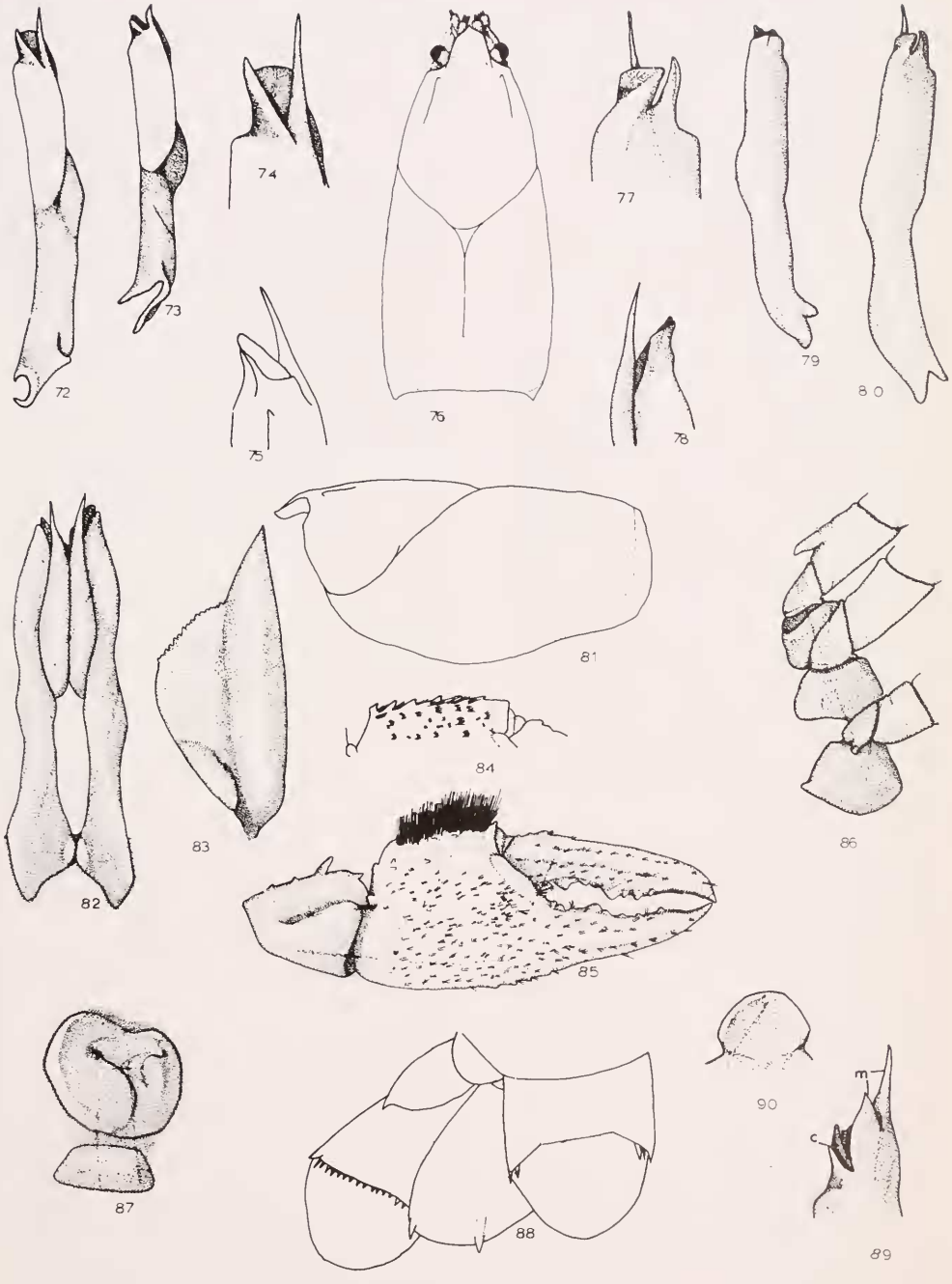
Hooks on ischia of third pereiopods only (Fig. 86); hooks simple, directed proximally and projecting to about midlength of basis. Coxae of third, fourth and fifth pereiopods lacking prominences or bosses.

First pleopods (Fig. 72, 74, 75, 77, 78, 80, 82) slightly asymmetrical and as described in *"Diagnosis"*; central projection and caudal process corneous.

Uropod (Fig. 88) with protopodite with small acute spine; mesial ramus with two spines projecting beyond distal margin, one from lateral angle and second of approximately same size from median ridge.

Sternum between third, fourth and fifth

Figures 72-90. *Procambarus (Girardiella) connus* n. sp.:72, mesial view of first pleopod of holotypic male, Form I; 73, terminal elements of first pleopod of morphotypic male, Form II; 74, terminal elements of first pleopod of holotype, mesial view; 75, terminal elements of first pleopod of holotype, cephalic view; 76, dorsal view of carapace of holotype; 77, terminal elements of first pleopod of holotype, lateral view; 78, terminal elements of first pleopod of holotype, caudal view; 79, lateral view of first pleopod of morphotype; 80, lateral view of first pleopod of holotype; 81, lateral view of carapace of holotype; 82, caudal view of first pleopods of holotype; 83, antennal scale of holotype; 84, mesial margin of palm of allotype; 85, distal podomeres of cheliped of holotype; 86, proximal podomeres of third through fifth pereiopods of holotype; 87, annulus ventralis and postannular sternite of allotype; 88, telson and left uropod of holotype; 89, mesial view of aberrant terminal elements of paratypic male, Form I (c = central projection, m = mesial process); 90, cephalic portion of epistome of holotype.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pereiopods moderately deep and bearing long setae partially obscuring first pleopod when held under thorax.

Morphotypic male, Form II. – Differing from holotype in following respects: mesial margin of left cheliped not so densely bearded as holotype; carpus of cheliped with additional spine along mesial margin (three total); right cheliped lacking beard, with only three tubercles in mesial row on margin of palm; latter apparently regenerated; cephalic portion of telson with only two spines in right caudolateral corner. Terminal elements of first pleopod (Fig. 73, 79) not corneous and less prominent than in holotype. Hooks of ischia of third pereiopods reduced markedly, almost tubercles.

Allotypic female. – Differing from holotype in following respects: mesial margin of palm (Fig. 84) with mesial row of seven spiniform tubercles and second, more median row of six squamous tubercles, margin provided with several squamous setiferous tubercles but no beard evident. Cephalic section of telson with only two spines in right caudolateral corner; sternites associated with third to fifth pereiopods not so deeply excavate, likewise, setae much reduced.

Annulus ventralis (Fig. 87) with broad centrocephalic excavation and set off cephalically by groove; prominent, but smooth cephalolateral ridges rising (ventrally) above sulcus, right continuing as lower ridge to midcaudal line; sinus originating cephalolateral to midline and arcing sinistrally to be lost in caudal fourth of annulus. Postannular sternite subtrapezoidal in outline and not highly elevated.

Types. – USNM nos. 146261, 146262, and 146263 (holo-, allo, and morphotype, respectively); *Paratypes:* Carroll County, Mississippi (47 ♂♂I). Paratypes at USNM.

Type-locality. – Carrollton, Carroll County, Mississippi.

Range. – *P. connus* is known only from the environs of Carrollton, Carroll County, Mississippi. This species is the only member of this group found associated with loess, being located in an area of brown loam and thick loess. Although Carrollton is in the Red Hills, remnants of the mantle do occur in the vicinity, too close to be ignored.

Color. – No color records for this species exist.

Variation. – Morphometric analysis was based on 44 Form I males. Carapace length was 26.6-41.0 (avg. 34.15). Rostrum length was 3.45-6.34 (avg. 5.31) and width was 1.08-1.58 (avg. 1.38). The length of the areola was 1.71-2.57 (avg. 2.40) and the length of the antennal scale was 6.05-9.31 (avg. 8.24). Chela length was 0.99-1.47 (avg. 1.37) and chela width was 2.09-2.59 (avg. 2.35). Length of the mesial margin of the palm and length of the dactyl were 2.38-2.82 (avg. 2.63) and 1.40-4.65 (avg. 1.81), respectively. Pleopod length was 2.51-3.84 (avg. 3.35).

In the topotypic series, one male of 17 had the mesial margin of the palm of the left cheliped almost devoid of setae; the right cheliped of this specimen and all the remaining specimens were like the holotype. In a second paratypic collection, one of 14 males had both chelipeds devoid of setiferous ornamentation (thus resembling *hagenianus*), and the ischia of the third maxillipeds were likewise devoid of dense setiferous beards. In the third paratypic series one of 17 males had a clearly regenerated hand which was lacking the beard of the inner margin of the palm; two had a straight mesial process. Otherwise, variation fell within the limits established in the diagnosis and descriptions outlined above. In one male, Form I, the terminal elements of the left first pleopod were markedly aberrant (Fig. 89); whether or not this was the result of an injury could not be ascertained.

Specimens examined. – MISSISSIPPI: Carroll Co., Carrollton, no date (17 ♂♂I, 1 ♂II, 1 ♀), (14 ♂♂I), (17 ♂♂I).

Remarks. – *P. connus* seems almost as closely related to *P. h. hagenianus* as is *P. h. vesticeps*. Indeed, I would say as closely were it not for the fact that apparent intergrade populations exist between the latter two. I find no suggestion that a zone of intergradation exists between *P. hagenianus* and *P. connus*. Therefore, I have taken the more conservative position, designating *connus* a species. Should intergrade populations be discovered subsequently, a minor

nomenclatorial change will rectify the situation. Although the degree of relationship existing between *P. h. hagenianus, P. h. vesticeps* and *P. connus* is not as precisely delimited as one might wish, each population represents a morphologically and geographically distinct entity as indicated more thoroughly in the "Discussion" section following.

Etymology. – The name of this species is taken from *konnos* (Gr.): a beard: this is in reference to the bearding of the mesial margin of the palm in males and the bearding of the third maxilliped.

Procambarus (Girardiella) pogum n. sp.
Figures 91-108

Cambarus (Girardiella) hagenianus carri Lyle, 1938:76, *nom. nud.*

Procambarus hagenianus. – Hobbs, 1968:K25 (Fig. 19c); Fitzpatrick, 1968:37 (part).

Procambarus (Girardiella) hagenianus. – Hobbs, 1972b:47 (part), 151 (part), 154 (part) (by implication).

Procambarus (Girardiella) sp. D. – Fitzpatrick, 1975:385, 386, 387, 388.

Diagnosis. – Body pigmented, eyes small but well-developed. Rostrum with subparallel to gently converging margins, lacking marginal spines; acumen short, indistinctly delimited basally. Areola 38.36-41.72 (avg. 39.69)% of entire length of carapace; areola linear. Carapace devoid of cervical spines or tubercles. Suborbital angle lacking. Postorbital ridges lacking spines or tubercles cephalically. Antennal scale 2.21-3.08 (avg. 2.62) times longer than wide, widest distal to midlength, thickened lateral portion terminating in strong, acute spine. Mesial margin of palm provided with dense setiferous beard, tubercles obscure; movable finger with relatively dense tuft of setae in basal third, tuft obscuring three or four small tubercles. Opposable margin of immovable finger with row of one large and one small tubercle in basal third and third tubercle at base of distal third, distal third with crowded minute denticles; opposable margin of movable finger with row of two small, one large and one small tubercle in basal half, small tubercle at base of distal third with crowded minute denticles distal to it. Ischia of third pereiopods only with stout spine; no prominences or bosses on coxae of third through fifth pereiopods. Mesial ramus of uropod with two conspicuous spines protruding beyond distal margin. First pleopods asymmetrical, shoulder weak at base of central projection; pleopods reaching midlength of coxae of third pereiopods when abdomen flexed; distal extremity bearing (1) prominent, subacute mesial process directed distally and slightly mesially, curved caudally in distal half, extending beyond other terminal elements; (2) well-developed central projection with apical portion directed laterodistally; and (3) prominent subrhombiform (in lateral aspect) caudal process extending distally not quite so far as central projection, distal margin sloped gently caudad and caudodistal margin lamelliform. Annulus ventralis of female deeply excavate centrocephalically with strong cephalolateral ridges terminating (ventrally) without tubercles; sinus originating slightly cephalic to center of annulus, arcing gently to be lost in caudal 10% of annulus; postannular sternite broadly conical in shape.

Holotypic male, Form I. – Body subovate, distinctly compressed. Abdomen narrower than thorax (9.3 and 14.1 mm). Width of carapace at caudodorsal margin of cervical groove less than height (14.1, 14.5 mm). Areola 38.46% of total length of carapace and linear; cephalic section of carapace 1.6 times as long as areola (Fig. 95). Rostrum sharply depressed (Fig. 101), deeply excavate dorsally, with thickened lateral margins slightly converging cephalically, marginal spines
basally; upper surface sparsely punctate, usual submarginal row of setiferous punctations present. Subrostral ridges moderately well-developed to level of antennae and visible to approximate distal third of rostrum in dorsal aspect. Suborbital angle lacking. Branchiostegal spine much reduced. Carapace sparsely punctate dorsally and laterally; granulate cephalolaterally with granulations best developed just posterior to orbit and antennal scale. Cervical spines or tubercles absent. Cephalic section of telson with two spines in each caudolateral corner

(Fig. 107). Cephalic portion of epistome (Fig. 105) subovoid in outline, about as broad as long, with small cephalomedian tubercle. Antennules of usual form with well-developed spine on ventral surface of basal segment slightly distal to midlength. Antennae broken, but apparently reaching to about caudal margin of carapace; antennal scale (Fig. 106) 2.73 times longer than wide, widest distal to midlength; thickened lateral portion terminating cephalically in stout, acute spine approximately 24% of total length of antennal scale; cephalic half of mesial margin of lamellar portion provided with numerous tubercular eminences bearing tufts of setae.

Ischia of third maxillipeds with long, stiff, unmatted, dense setae arising from mesial and ventrolateral margins.

Right chela (Fig. 104) with palm inflated, moderately depressed; lateral margin nearly straight, not costate; entire palmar area covered with setiferous punctations; mesial margin of palm with mat of dense setae obscuring tubercles; row of six squamous tubercles medial to setiferous beard; mesial margin of movable finger with tuft of setae in proximal third partially obscuring row of three low tubercles. Opposable margin of movable finger slightly excavated on basal one-third; with row of two small, one large and one small tubercle in basal one-half; small tubercle at base of distal third with crowded minute denticles between it and tip of finger; finger with submedian longitudinal ridge above and below, both flanked by setiferous punctations. Opposable margin of immovable finger with row of one large, one small and two nearly inconspicuous tubercles in basal half; moderate sized tubercle at base of distal third directed ventromedially, crowded minute denticles between it and tip of finger; finger with submedian longitudinal ridge above and below, both flanked by setiferous punctations.

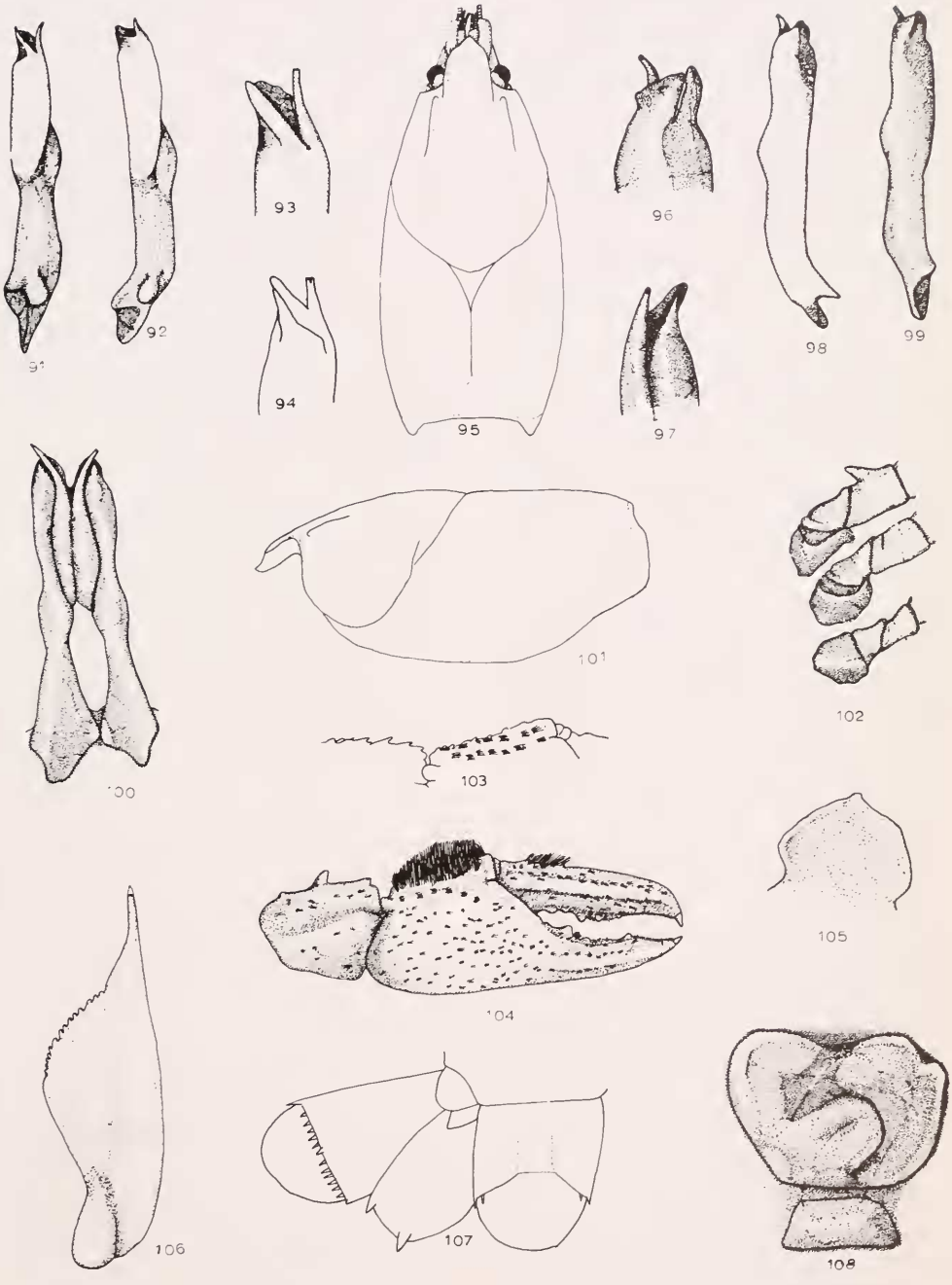
Carpus of right cheliped longer than broad with mesial margin bearing single strong acute spine slightly distal to midlength, two smaller equally spaced acute spines proximal to it, row of four squamous setiferous tubercles along middle third of mesial portion of carpus medial to aforementioned spines, small subacute spine in mesiodistal corner; punctate dorsally with longitudinal furrow slightly mesial to midline; lower distal margin with acute spines in each corner and row of three low, almost tubercular, spines between distal ventromesial corner and stout spine of mesial margin.

Merus of right cheliped with dorsal row of six tubercles terminating distally in two acute spines (distalmost strongest); ventromesial margin with row of 13 acute spines increasing in size distally; ventrolateral margin with row of seven spines, increasing in size distally. Mesial margin of ischium with row of three small but acute spines decreasing in size distally.

Hooks on ischia of third pereiopods only (Fig. 102); hooks simple and directed proximocephalically, extending just beyond distal margin of basis; coxae of third, fourth and fifth pereiopods lacking prominences or bosses.

First pleopod (Figs. 91, 93, 94, 96, 97, 99, 100) as described in *"Diagnosis"*; central projection and caudal process corneous.

Figures 91-108. *Procambarus (Girardiella) pogum* n. sp.: 91, mesial view of first pleopod of holotypic male, Form I; 92, mesial view of first pleopod of morphotypic male, Form II; 93, terminal elements of first pleopod of holotype, mesial view; 94, terminal elements of first pleopod of holotype, cephalic view; 95, dorsal view of carapace of holotype; 96, terminal elements of first pleopod of holotype, lateral view; 97, terminal elements of first pleopod of holotype, caudal view; 98, lateral view of first pleopod of morphotype; 99, lateral view of first pleopod of holotype; 100, caudal view of first pleopods of holotype; 101, lateral view of carapace of holotype; 102, proximal podomeres of third through fifth pereiopods of holotype; 103, mesial margin of palm of allotype; 104, distal podomeres of cheliped of holotype; 105, cephalic portion of epistome of holotype; 106, antennal scale of holotype; 107, telson and left uropod of holotype; 108, annulus ventralis and postannular sternite of allotype.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Uropods (Fig. 107) with mesial ramus bearing two spines projecting beyond distal margin, one from lateral corner and one, slightly larger, from median ridge.

Sternites and coxae of third through fifth pereiopodal segments bearing setae partially obscuring pleopods when latter held under thorax.

Morphotypic male, Form II. – Differing from holotype in following respects: mesial margin of palm with setiferous mat not so dense, but still obscuring margins completely; lacking tuft of setae on mesial margin of dactyl; hooks on ischia of third pereiopods not so strong, almost tubercular. Terminal elements of first pleopod (Fig. 92, 98) nonconeous, proportionately smaller and less developed; base of central projection enveloped by tightly applied fold on mesial, cephalic and lateral surfaces. Setiferous ornamentation of pereiopodal sternites and coxae less well-developed. Tip of rostrum markedly more truncate (broken early in life?).

Allotypic female. – Differing from holotype in following respects: mesial margin of palm (Fig. 103) and dactyl lacking setiferous beard, instead palm with mesial row of six tubercles and with two rows of seven each squamous setiferous tubercles median to it; row of nine spinose tubercles median to stout spine of mesial margin of carpus giving serrated appearance to upper mesial edge; spines between stout mesial spine and distal ventromesial spine of carpus strongly acute, additional row of four spines ventromesial to aforementioned spines and row of two ventromesial to stout spine of mesial margin.

Annulus ventralis (Fig. 108) deeply excavate centrocephalically, sulcus sloping precipitously cephalically; annulus set off cephalically by deep groove; quite large cephalolateral ridges lacking tubercles, extending ventrally approximately three times depth of remainder of annulus; sinus originating slightly cephalic to center of annulus and forming gentle arc sinistrally to be lost in caudal 10% of annulus; postannular sternite broadly subconical in shape.

Types. – USNM nos. 146270, 146271, and 146272 (holo-, allo-, and morphotypes, respectively); *Paratypes:* Chickasaw County, Mississippi (2 ♂♂I, 4 ♂♂II, 9♀♀). Paratypes are located at the National Museum of Natural History.

Type-locality. – Houston, Chickasaw County, Mississippi.

Range. – The species is known only from burrows at the type-locality and from 0.4 mi E of Houlka Creek where the animals were taken from burrows in a roadside ditch. The latter, the only precise locality, is associated with the Ripley formation. Apparently *P. pogum* is associated with the upper coastal plain of the Tibbie Creek drainage.

Color. – The basic color pattern of *P. pogum* is reddish, infused with henna and with lighter areas associated with the lateral carapace, the rostral margins and the postorbital ridges.

Variation. – The limits of variation as known are incorporated into the diagnosis and description sections above. Morphometric analysis was based on a total of 15 specimens (2 ♂♂I, 4 ♂♂II, 9 ♀♀). Carapace length in Form I males was 28.6-31.1, for females 26.4-37.4 (avg. 32.51) and for Form II males 24.8-34.0 (avg. 28.8). Rostrum length was 3.36-4.85 in Form I males, 4.24-5.45 (avg. 4.85) in females and 4.20-5.26 (avg. 4.59) in Form II males; width of the rostrum was 1.39-1.77, 1.17-1.51 (avg. 1.37) and 1.23-1.59 (avg. 1.41) in the same three categories, respectively. Areola length was in Form I males 2.55-2.60, in females 2.40-2.61 (avg. 2.52) and in Form II males 2.45-2.53 (avg. 2.46). Antennal scale length was 6.98-7.97 in Form I males, 7.33-9.42 (avg. 8.34) in females and 7.18-9.16 (avg. 8.37) in Form II males. Chela length was 1.48-1.51 in Form I males, 1.57-4.03 (avg. 2.01) in females and 1.67-2.03 (avg. 1.80) in Form II males; chela width in Form I males was 1.47-2.53, 0.45-2.44 (avg. 2.11) in females and 2.45-2.60 (avg. 2.53) in Form II males. Length of the mesial margin of the palm and length of the dactyl in Form I males were 2.76-3.44 and 1.58-1.68, respectively. The same two characteristics in the same sequence were in females 1.10-2.72 (avg. 2.45) and 0.76-1.72 (avg. 1.55); in Form II males

they were 2.65-2.93 (avg. 2.78) and 1.51-1.76 (avg. 1.61). Pleopod length in Form I males was 2.18-3.21 and in Form II males was 3.64-3.74 (avg. 3.68).

Specimens examined. – MISSISSIPPI: Chickasaw Co., Houston, 11 April 1936 (2 ♂♂I, 3 ♂♂II, 8 ♀♀), 0.4 mi E of Houlka Creek, no date (1 ♂II, 1 ♀).

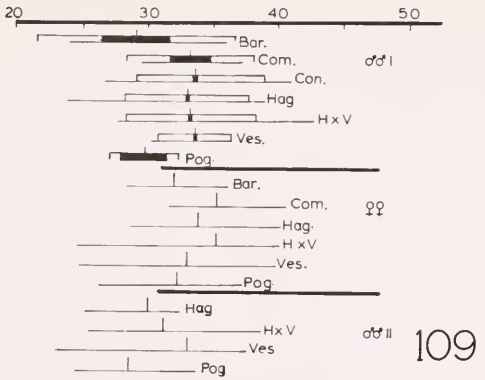
Etymology. – Taken from *pogon* (Gr.): beard; in reference to the setiferous beard found on the mesial margin of the hands in males and on the third maxilliped.

DISCUSSION

Each of the taxa described here, except *P. h. vesticeps*, probably represents a distinct breeding population of crawfish. There are many morphological features which distinguish each of the populations; likewise, there are no, again with the exception of *vesticeps*, evidences of intergradation. In each instance there seems to be either differences in ecological habitat preferences and/or physical disjunction of the habitat. Morphometric analyses strongly support the conclusions offered for other kinds of data and reveal that the several species are no more variable than other crawfish species similarly studied, exhibited no greater interspecific variation within a taxonomically compact grouping and exhibited no evidence of clines.

The most taxonomically significant differences can be found in the details of the terminal elements of the first pleopod of the Form I males. In *P. hagenianus hagenianus* and *P. h. vesticeps* the centro-cephalic process is enveloped at its base by a tight fold which becomes continuous with the centro-caudal process. A similar, but not so tightly applied, fold wraps the lateral base of the centro-cephalic process in *P. barbiger*. Contrastingly, in *P. connus* the anterior base of the cephalic portions of the centro-cephalic process has a tightly applied fold, but the fold is absent from the lateral portions. In *P. cometes* and *P. pogum* such a fold is absent. In all populations the caudal process is a broad, truncate extrusion, laterally compressed in its caudodistal half. The caudodistal margin of all, except *barbiger*, forms an angular intersection with the distal margin; in the latter this intersection is curvilinear. Only in *P. h. hagenianus*, however, is the distal margin subperpendicular to the main axis of the shaft; in all other species the margin is gently sloping, and in no species does the caudal process project distally as far as the central projection. The mesial process in all is a long, subconical, nearly setiferous protrusion extending, except in *cometes*, well beyond the distalmost portions of the other terminal elements; in *cometes* it extends distad approximately the same distance as the central projection. Only in *P. connus* is the mesial process subparallel to the main shaft of the appendage. In *P. cometes* it is curved sharply laterad, and in the remaining species it is curved gently laterad. A caudally oriented curve of the mesial process exists, additionally, in both subspecies of *hagenianus*, in *barbiger* and in *connus*, whereas in *pogum* the process curves gently cephalad to recurve gently caudad in its distal half. A pronounced shoulder occurs at the base of the cephalic margin of the central projection in both subspecies of *hagenianus*, in *barbiger* and in *connus*, although it is not sharply angular in *vesticeps* and *barbiger*. In other details the appendages are as outlined in the diagnoses above and are similar.

The most conspicuous feature of the previously undescribed taxa is the beard of plumose setae along the entire mesial margin of the palm. Such pubescence is also present in varying degrees (varying according to species) on the dactyl, on Form II males and on females, but is best developed in Form I males. All of the species bear a dense double row of plumose setae along the surface of all units of the third maxilliped. This characteristic is sufficiently common in species of primary burrowing habits to suggest an adaptation to such an habit. In *P. barbiger* and *P. pogum* the ventrolateral surface of the exopodite of the third maxilliped is provided with a dense row of heavy, stout setae forming a mat. In *P. cometes*, *P. connus* and *P. h. vesticeps* the setae of this row are stout but markedly more sparsely distributed. In *P. h. hagenianus* the row is usually absent,



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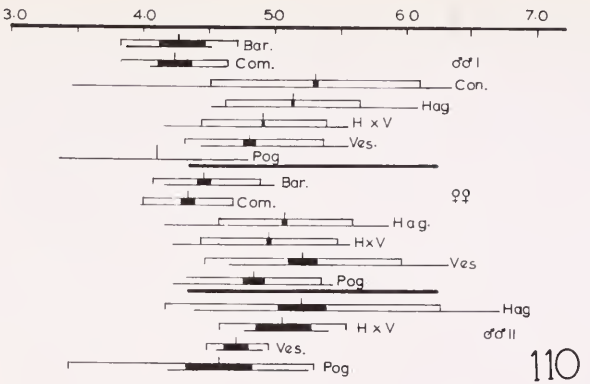

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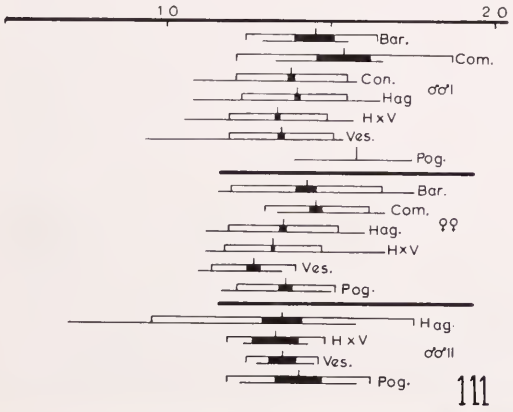

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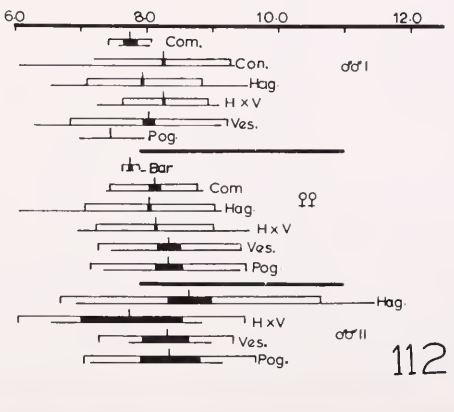

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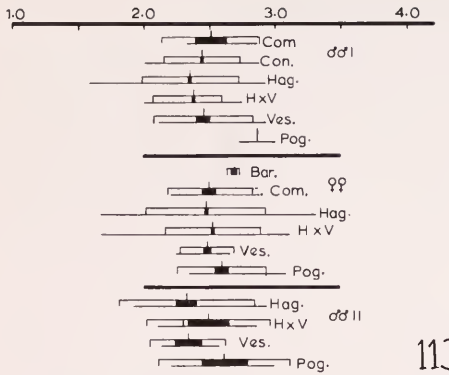
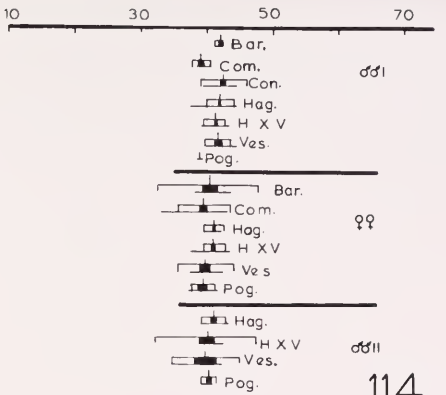
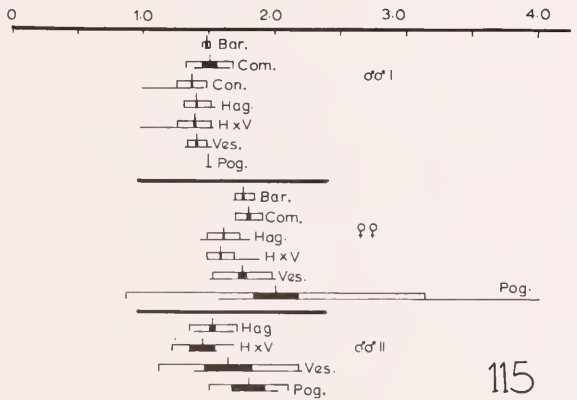
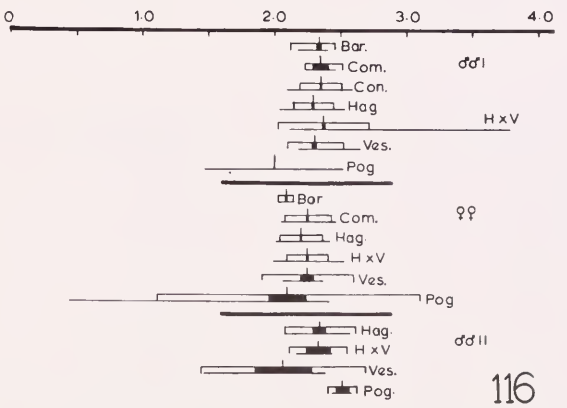
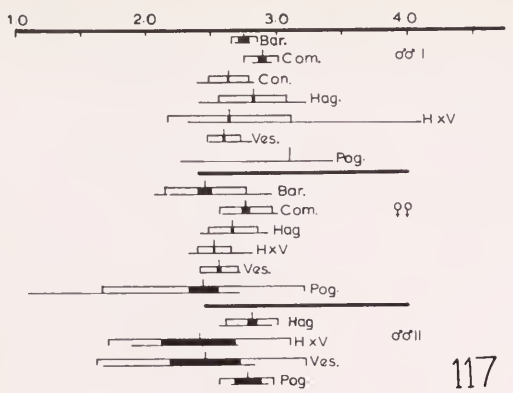








Figures 109-119. Morphometric variation in Hagenianus Group crawfishes (horizontal lines = range, vertical lines = mean, solid horizontal bars = 2 standard errors of mean, open horizontal bars = 1.5 standard deviations); species abbreviations are: Bar. = *P. (G.) barbiger,* Com. = *P. (G.) cometes,* Con. = *P. (G.) connus,* Hag. = *P. (G.) h. hagenianus,* H x V = *P. (G.) h. hagenianus* x *vesticeps,* Ves. = *P. (G.) h. vesticeps,* Pog. = *P. (G.) pogum;* ratios as described in text: 109, carapace length (in mm); 110, rostrum length; 111, rostrum width; 112, antennal scale length; 113, antennal scale width; 114, areola length (as % length of carapace); 115, chela length; 116, width of palm; 117, length of inner margin of palm; 118, dactyl length; 119, pleopod length of males.



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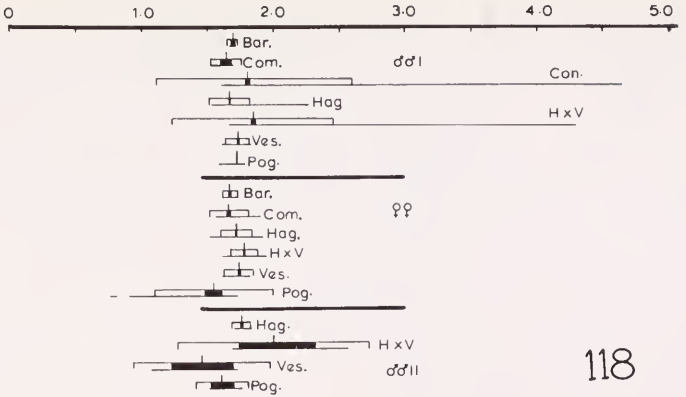

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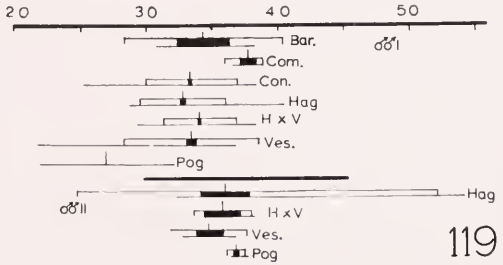

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Figures 109-119. Morphometric variation in Hagenianus Group crawfishes. Legend on Preceeding page.

but if present, at best consists of a very thin row of delicate setae.

The antennal scale reflects the degree of setation found along the hand of Form I males in every species. In *P. h. hagenianus* the setae are restricted to the short bristles common along the mesial margin in most crawfishes. In *P. barbiger* they are longer and stouter; in all of the other taxa the mesiocephalic margin is provided with tufts of long setae arising from tubercular eminences on the margins. The antennal scale is widest approximately at midlength in *P. barbiger, P. cometes, P. connus* and *P. pogum,* but it is widest distal to midlength in the subspecies of *P. hagenianus.* In all taxa the thickened lateral margin terminates distally in a strong acute spine, although the relative length of the spine varies according to the species. In *P. barbiger, P. cometes* and *P. pogum* it constitutes about 33% of the total length of the scale; in *P. connus* it is about 25% of the length; and it is about 10-15% in the subspecies of *P. hagenianus.* The spine is markedly more attenuate in the first three mentioned species than in the others and reaches the other extreme in *P. h. vesticeps* in which it is nearly conical in shape. Other variations are mentioned in previous discussions.

A much more difficult characteristic to evaluate is the annulus ventralis of the female. All have an annulus in which there is an anterior trough (sulcus) which rises caudally; the highest (ventrally) portions are cephalolateral and/or lateral, and the annulus is movable; usually the prominences are decorated with tubercular eminences. In the subspecies of *P. hagenianus* and in *P. pogum* the anterior portion of the sulcus slopes precipitously toward a deeply excavate sternum associated with the fourth pereiopodal segment. The annulus is poorly delineated from the sternum associated with its anterior margin in the subspecies of *P. hagenianus,* but in *P. pogum* is set off by an intervening groove. The annulus of *P. barbiger* has a less severe slope and is delineated anteriorly from the sternite by a groove. In *P. cometes* the anterior sulcus is narrow, less sloped and delimited anteriorly by a groove. The postannular sternite (associated with pereiopodal segment V) is subconical in *P. h. hagenianus* and *P. cometes,* broadly conical in *P. h. vesticeps* and *P. pogum,* but in *P. barbiger* is in the shape of a triangular prism.

In morphometric analysis 10 characteristics were analyzed in males and nine in females. For analysis the males were treated as two separate categories — Form I and Form II. Thus, 29 comparisons could be made between any two populations. When these comparisons were made using a null hypothesis, the following significant ($p \geq 0.05$) differences were established (Table 1): *P. h. hagenianus* differed from *P. h. vesticeps* in 24 characteristics, from *P. barbiger* in 14 (of 19), from *P. connus* in 5 (of 10), from *P. pogum* in 21 and from *P. cometes* in 14 (of 19). *P. h. vesticeps* differed from *barbiger* in 10 (of 19), from *connus* in 8 (of 10), from *pogum* in 21 and from *cometes* in 18 (of 19). *P. barbiger* differed from *connus* in 4 (of 19), from *pogum* in 7 (of 10) and from *cometes* in 6 (of 19). *P. connus* differed from *pogum* in 6 (of 10) and from *cometes* in 7 (of 10); and *P. pogum* differed from *P. cometes* in 12 (of 19). In many of these $p \geq 0.01$. The report of less than all possible combinations results from the fact that no Form II males are known for *P. barbiger,* and there are insufficient numbers for analysis in the category of Form II males for *P. cometes* and *P. connus* and for females in *P. connus.*

Procambarus barbiger and *P. connus* seem to be geographically isolated from the other species, and the latter is the only one associated with loess. The subspecies of *P. hagenianus* are apparently restricted to the prairie soils of the Black Belt of Alabama and Mississippi, with the nominate subspecies occupying the area south and east of Tibbie Creek, a tributary to the west bank of the Tombigbee River in east-central Mississippi; an intergrade population occurring just north of the creek; and *P. h. vesticeps* being confined to the upper Tombigbee River system (Fig. 120). *P. cometes* and *P. pogum* occupy limited areas in different habitats just outside the periphery of the range of *P. hagenianus;* both are associated with the interior flatwoods.

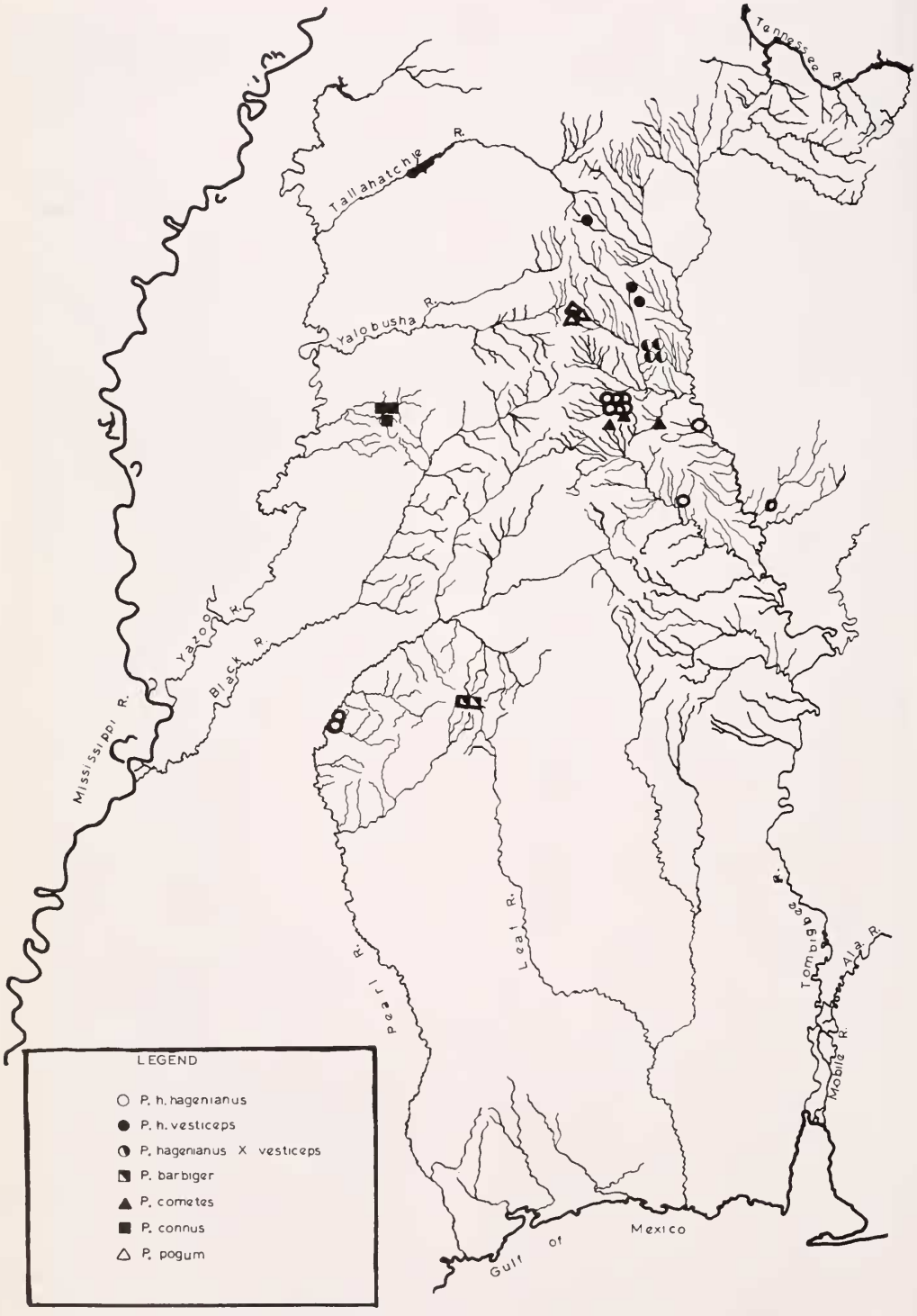

Figure 120. Distribution of Hagenianus Group crawfishes.

The species of the Hagenianus Group probably represent a derivative stock rather than an ancestral stock within the subgenus *Girardiella*. The loss of the cephalic process, present in all other species of the subgenus, is an excellent indication that this group is unlike the ancestral stock. Four taxa–*h. hagenianus, h. vesticeps, barbiger* and *connus*–possess a highly specialized structure in the fold which envelops the base of the central projection. All Hagenianus Group species have a nearly unique spinose ornamentation on the uropods, indicating a secondarily acquired characteristic. In the subgenus, the most generalized pleopod is probably found in *Procambarus (Girardiella) gracilis*, but the relatively broad areola found in *P. (G.) tulanei* is generally considered to be a more primitive condition in crawfishes than the obliterated or linear areolae characteristic of species of the subgenus. Bearding of the hands and maxillipeds is a more widespread phenomenon, but general consensus favors the unbearded hand as the more primitive condition in crawfishes. *P. tulanei* becomes interesting in a study of the Hagenianus Group because it seems to fill certain essential criteria as a form intermediate between the two species complexes constituting the Gracilis and Hagenianus Groups. Geographically, it is found in the Red and Ouachita River systems of Arkansas and Louisiana; the other taxa of the Gracilis Group are found in an arc and are northeast to southwest of it. It is the only member of this assemblage with a beard of long setae along the mesial margin of the palm, while *P. h. hagenianus* is the only member of the Hagenianus Group to lack it. The broad areola has already been mentioned. Thus, as I have previously outlined (Fitzpatrick, 1975), a *tulanei*-like stock is not an unreasonable candidate for the ancestral population, the Gracilis Group constituting modern descendants most like the ancestor.

The routes by which the Hagenianus Group populations came to occupy the present habitats are difficult to assess. Two possible avenues of invasion exist. They may have come by a southerly route, or they may have come from the northwest, crossing the Mississippi River in the vicinity of Memphis or likely more northward. The former route, with a crossing associated with the Vicksburg-Natchez area, is unlikely. To perform a southerly crossing they would have had to cross a relatively wide band of loess, a type of material not well suited to primary burrowing crawfishes. Another problem to their dispersal is the intervening flood plain of the river. Everywhere south of the confluence with the Ohio River this flood plain is quite wide, but south of Memphis, excepting the Natchez area, it becomes even wider to develop into the extensive Delta Plain of southern Louisiana. Fitzpatrick and Hobbs III (1968) have argued that the Mississippi River acts as a zoogeographical barrier to the dispersal of certain species of crawfishes and probably other aquatics principally by the interposition of the flood plain as an ecological barrier. Thus, direct connection between the *tulanei* population progenitors and the Hagenianus Group ancestors in an east-west pattern is quite unlikely.

On the other hand, the species complex currently identified as *gracilis* occurs, in part, east of the river north of the Ohio River confluence. Broad bands of Tertiary and Cretaceous deposits can be found in western Tennessee and Kentucky. A more likely avenue for invasion, then, may be associated with these features. Thus, the prairie substrate can be seen as exploitation of an available habitat rather than a center from which expansion occurred. The habitat of *P. connus* is probably not the source from which radiation occurred. The loess and/or sandy substrates around Carrollton are not suited to a primary burrower. Several morphological features of *P. cometes* suggest that it does not represent the ancestral population. The mesial process of the first pleopod of the Form I male is subequal to the central projection, a condition unique in the subgenus. The sulcus of the annulis vertralis is markedly more narrow than in any of the related species, and the first pleopod lacks a shoulder on the cephalic surface near the base of the central projection.

As noted, the subspecies of *P. hagenianus* have many specializations which indicate

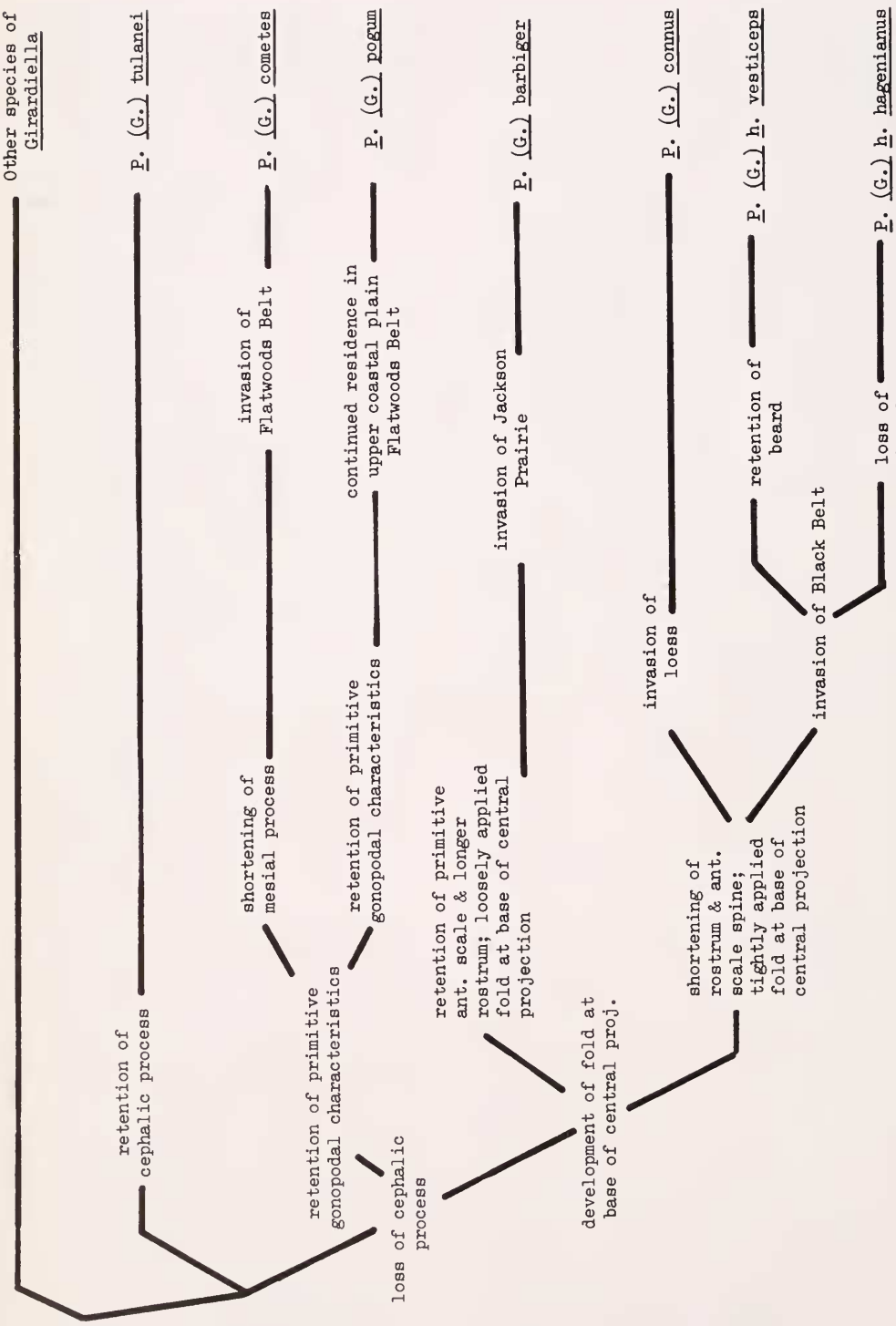

Figure 121. Proposed relationships of Hagenianus Group crawfishes.

that they do not represent the population from which the Hagenianus Group stock descended, and their prairie soil habitat does not represent a continuum through which invasion could take place. Although *P. barbiger* seems to retain several features which associate it with the primitive stock (bearded hand, lamellar portion of antennal scale lacking a tubercular margin, and a groove at the anterior margin of the annulus), it also has some unique and probably derived characteristics: the beard of the hand occurs in distinct tufts; the distal margin of the caudal process has a curvilinear relationship with the caudal margin rather than angular; the lateral base of the central projection is covered by a loosely applied fold; and the postannular sternite is uniquely in the shape of a triangular prism. Couple these morphological features with the prairie-habitat difficulty mentioned above, and one is inevitably drawn to the conclusion that this species represents a secondary, albeit early, invasion of an available habitat.

Thus, one is left with one species, *P. pogum*, having relatively primitive characteristics within the group and occupying a habitat compatible with an environmentally plausible invasion route. But *pogum* does not in itself represent a relict of the ancestral stock. Several features indicate that it, too, has undergone specialization. The shoulder at the base of the central projection is lacking in *pogum* and only one other species in the subgenus, *cometes*. Only in *pogum* in the Hagenianus Group is the mesial process recurved distally, and the slope of the sulcus of the annulus ventralis falling precipitously toward the anterior margin is more like the derivative *hagenianus* populations than the other species. The antennal scale is an excellent structure to indicate the mixed combination of characters found in this species: primitive features include a long spine forming the distalmost part of the thickened lateral portion (33% as in *barbiger* and *cometes*, compared with 25% in *connus* and 10-15% in the subspecies of *hagenianus*) and being widest near midlength (as in *barbiger*, *cometes* and *connus*). On the other hand, it shares the apparently derived condition of having setae arising in tufts from tubercular prominences along the cephalic portion of the lamellar margin with *cometes*, *connus* and *h. vesticeps*.

The picture presented, then, is one in which a crawfish stock entered the area across the Mississippi Flood Plain from the northwest probably in a single invasion. But shortly after invasion an adaptive radiation occurred resulting in the reproductive isolation of five populations, with the easternmost filling the most expansive habitat and undergoing clinal (?) variation which eventually resulted in geographic races. Suggested relationships are given in Figure 121.

A Key to the Hagenianus Group of Crawfishes

In Hobbs' (1972b:45) "Key to Species of Subgenus *Girardiella*," couplet 1 must be modified as follows (*italics* indicate changes):

1 Mesial surface of palm of chela bearded; areola *always* with 3 or 4 punctations across narrowest part; *cephalic process present* . . . . . *P. (G.) tulanei* Penn.

Mesial surface of palm of chela never bearded, *or if bearded areola linear and cephalic process absent*, areola linear or with only 1 or 2 punctations across narrowest part. . . . . 2.

The keys here offered may then be used following identification of *P. hagenianus* in couplet 4. Alternately, after eliminating the genus *Fallicambarus* and the subgenus *Acucauda* from consideration, one may proceed directly to this key if the specimens possess a median spine extending beyond the distal margin of the inner ramus of the uropod.

1	Sex male	2.
1'	Sex female	7.
2 (1)	Mesial margin of palm with setiferous beard.	3.
2'	Mesial margin of palm lacking setiferous beard. . . . . *P. h. hagenianus* (Faxon).	
3 (2)	One or more tufts of long setae arising along mesial margin in basal half of dactyl.	4.
3'	Dactyl lacking tufts of long setae along mesial margin.	5.

4 (3) Tufts of setae on dactyl scanty; tight fold enveloping base of central projection in Form I male. . . . . *P. connus* n. sp.

4' Tufts of setae on dactyl well-developed; base of central projection of Form I male lacking enveloping fold. . . . . *P. pogum* n. sp.

5 (3') Mesial process of first pleopod subequal to central projection in length; lacking enveloping fold at base of central projection in Form I males. . . . . *P. cometes* n. sp.

5' Mesial process of first pleopod longer than central projection; base of central projection enveloped by fold in Form I males. . . . . 6.

6 (5') Distal margin of caudal process of first pleopod subperpendicular to main axis of shaft of pleopod; setae of lamellar portion of antennal scale arising in tufts from tubercular eminences. . *P. h. vesticeps* n. subsp.

6' Distal margin of caudal process of first pleopod not subperpendicular to main axis of shaft of pleopod; setae of lamellar portion of antennal scale arising individually. . . . . *P. barbiger* n. sp.

7 (1') Antennal scale widest near midlength, distal spine of thickened lateral portion constituting at least one-fourth of total length of scale. . . . . 8.

7' Antennal scale widest distal to midlength, distal spine of thickened lateral portion constituting less than one-fourth of total length of scale. . . . . 11.

8 (7) Setae of lamellar portion of antennal scale arising in tufts from tubercular eminences; postannular sternite conical. . . . . 9.

8' Setae of lamellar portion of antennal scale arising individually; postannular sternite in shape of triangular prism. . . . . *P. barbiger* n. sp.

9 (8) Distal spine of thickened lateral portion of antennal scale constituting about one-third of total length of scale. . . . . 10.

9' Distal spine of thickened lateral portion of antennal scale constituting about one-fourth of total length of scale. . . . *P. connus* n. sp.

10 (9) Trough of annulus broad and descending precipitously cephalically toward sternites; postannular sternite broadly conical. . . . . *P. pogum* n. sp.

10' Trough of annulus narrow and subparallel to horizontal plane of sternites; postannular sternite subconical. . . . . *P. cometes* n. sp.

11 (7') Setae of lamellar portion of antennal scale arising in tufts from tubercular eminences; postannular sternite broadly conical. . . . . *P. h. vesticeps* n. subsp.

11' Setae of lamellar portion of antennal scale arising individually; post annular sternite subconical. . . . . *P. h. hagenianus* (Faxon).

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